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THE SCIENTIFIC BASIS
OF EVOLUTION

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OF
EVOLUTION

BY

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CONTENTS

Preface vii

Chapter Page

I. Introduction 13

II. The Cellular Basis of Heredity and Evolution 43

III. Mendelian Inheritance and its Relation to the Distribution of the Genes 61

IV. Variability and Artificial Selection 91

V. Adaptation and Natural Selection 109

VI. Mutation 132

VII. The Theory of Sexual Selection and Hormones 152

VIII. Embryonic Development and its Relation to Evolution 170

IX. The Inheritance of Acquired Characters 187

X. The Social Evolution of Man 203

XI. Evolution as a Response to "The Order of Nature" 218

XII. Mechanistic and Metaphysical Interpretations of Biology and of Evolution 238

References to Literature 255

Index 279

PREFACE

THE twelve chapters that follow represent the Messenger Lectures given at Cornell University in the spring of 1931. The lectures have been somewhat expanded but stand essentially as delivered. An attempt to cover briefly so wide a field leads to a somewhat superficial treatment of many of the highly technical subjects that are dealt with. In attempting to simplify the presentation I am aware that I may sometimes appear more dogmatic than the topics permit. The professional reader will, I trust, make generous allowance for shortcomings in this respect. If the technicalities make difficulties for other readers, this very fact may bring home another lesson, namely, that in biology the time has gone by when the discussion of the problems of evolution is supposed to be a field in which everybody can speculate without respect to the evidence at hand, and more particularly without any regard to the value of the kind of evidence on which an opinion can safely rest. It is, in fact, the main purpose of this book to insist that the study of evolution has become sufficiently advanced to rest our case for its acceptance on the same scientific procedure that has led to the great advances in chemistry and physics. Whether this procedure is called mechanistic or by some other name does not so much matter as does the recognition that only by experiment may we hope to rescue the theory of evolution from the vague speculative methods of its immediate past. It is mainly for this reason that I have in the last two chapters discussed the opinions of philosophers, metaphysicians, and mystics concerning organic evolution. My contention is that these speculations have not been helpful in finding out how evolution has come about. On the contrary, I think that these attempts to remove the problems from the biological field have done more harm than good, by their popular appeal to mysticism, and by directing attention away from the more laborious but safe procedure of studying the problem of evolution in the same way that other scientific problems are studied.

I am quite well aware that the standpoint taken with regard to a mechanistic interpretation of the evolution of living things may appear naïve in comparison with some of the subtle philosophical and metaphysical interpretations that have recently been offered as alternatives. Aware also that the use of the term "mechanistic" may, in the light of the recent developments in mathematical physics, expose my views to the opprobrium of materialism or of the older rigid interpretation of mechanism, but a careful reading of the text will, I hope, remove to some extent the implications sometimes imputed to those with mechanistic leanings. In the present state of the evolution theory a frankly naïve view may not be altogether a drawback if progress along scientific lines is looked upon as more worthwhile than a stultification of the whole field of investigation by arbitrary metaphysical subtleties.

I wish to express my appreciation to Dr. Th. Dobzhansky, who has read the manuscript and supplied many valuable suggestions; also to Dr. Albert Tyler, who has given helpful assistance. Dr. Henry Borsook has advised me on several critical points, as have Dr. A. H. Sturtevant, Dr. C. B. Bridges and Dr. Jack Schultz. My wife, Lillian V. Morgan, has assisted in many ways with the text.

The lectures were given to a University audience, hence it was possible to take for granted a certain amount of general information on the topic of evolution. It is hoped that as much may be taken for granted on the part of the educated public to which the book is now addressed.

THE SCIENTIFIC BASIS
OF EVOLUTION

CHAPTER I

INTRODUCTION

WITH the opening years of the present century evolution began to be seriously studied by experimental methods for the first time in its long history. In 1900, de Vries described the mutations of the evening primrose and in 1901 he brought forward a theory of evolution by mutation—a theory based on experimental procedure. In 1900, Mendel's paper on heredity came to light. Three years later (1903) Johannsen's work on pure lines appeared. It, too, was based on experiment. In the same year, Sutton first pointed out that the chromosome mechanism of the maturation stages of the egg and sperm-cell supply a mechanism that accounts for the two laws of heredity that Mendel had discovered. While the information relating to these stages of the maturation of the germ-cells was not based on experiment but was largely the result of direct observation, nevertheless some experimental work had been carried out that had made highly probable the view that the chromosomes are the bearers of the hereditary units. The evidence from these four sources and the subsequent developments furnish us today with ideas for an objective discussion of the theory of evolution in striking contrast to the older speculative method of treating evolution as a problem of history.

As a result of this work it is now realized that the most promising method for the interpretation of evolution is through an appeal to experiment. By an appeal to experiment is meant the application of the same kind of procedure that has long been recognized in the physical sciences as the most dependable one in formulating an interpretation of the outer world. I am aware, of course, that biologists who in the past have relied on this appeal, had supposed that in the physical sciences they had an anchor to windward. Recent developments in physics have been so extraordinary that, today, the biologist is left wondering whether he has anchored on a safe bottom. He is flattered for the moment, when the eminent mathematician and philosopher, Whitehead, discovers that the biological conception of organism is far more important for physicists than their traditional but narrow point of view, and when a mathematician and astronomer, Jeans, concludes that the Universe is Mind. Now the *human mind* is something that the biologist had hoped some day to study by the experimental approach. He would be immensely flattered to be told that he would then be engaged in the elucidation of something that extends out beyond the farthest star, were it not that he has become a little skeptical regarding the adequacy of metaphysical solutions of the cosmos based on introspection.

Impressed by these grand ideas, but left still in doubt, the working biologist will return to his shop to see whether there be not some safer way of finding out more about living things and their evolution. He will go back and try to discover whether there may not be much still to be learned from a method that he has come to respect from his experience, and leave the discussion of finalistic doctrines to metaphysicians and philosophers of sorts.

The question whether organic evolution has taken place in the past will not be discussed. Organic evolution means that the animals and plants at present living on the earth have descended from others living in the past, and that, in the course of time, a process of divergence has taken place—or, as we say, rather loosely, higher or more complex types have come from lower or simpler types. This theory of descent with modification has so much circumstantial evidence in its favor, and its probability is so great, that I do not believe it would be profitable to go over again what is contained in hundreds of available books on the subject. But when we consider the *causes of evolution* we get at once onto debatable ground, where the widest possible divergence of opinion exists, not only amongst biologists, but amongst other theorists who have ventured to make *ex cathedra* statements concerning the directive agents of evolution.

Until the present century the evidence on which the theory of descent rested was, as I have said, derived largely from observation, and was therefore for the most part descriptive. The theory was more of the order of a broad generalization than of a scientific theory based on controlled experimental data. As such, it could not but be contrasted, on the one hand, with the theories of the exact sciences of chemistry and physics, and, on the other, with finalistic theories which depend largely on ratiocination and metaphysics. The theory of organic evolution has suffered from both of these comparisons, for, on the one hand, it could not fully meet the exact requirements of scientific theory that chemistry and physics demand as the essential basis of their conclusions, namely, predictions that can be verified by means of quantitative data; and, on the other hand, it made no pretence of arriving at the ultimate or finalistic solution which philosophers adopt as their goal.

It was, however, not so much from these two sources that the theory of organic evolution met with its most serious opposition, but rather because it came into conflict with theological cosmogonies, whose principal claims to precedence were based on still other grounds.

The contest has continued to the present day on a wide front, or rather, on three fronts. The physical scientists have, on the whole, given evolution a fair hearing, but have not lost sight of the fact that, as a theory, it has not passed beyond the observational stage of development, and some physicists seem still to hold reservations when the theory is applied to the workings of the human mind, in which they seem to have the utmost confidence. The philosophers, too, have in most cases given the current theory of evolution a sympathetic hearing, but have assigned it to second place, relying rather on speculation to penetrate further into the interpretation of evolution than on mere description and testing of its, to them, superficial aspects.

While a few theologians have had the courage to accept those parts of the theory that relate to the continuity of organic life, they hesitate to conclude that evolution has been undirected, or even "mechanistic," and make an exception in the case of what is called man's "spiritual nature."

The theory has also suffered at the hands of its would-be friends who have sometimes made unjustifiable claims, both on the score of the validity of the evidence and of the wider deductions from the theory. Humanly speaking, it is understandable, I think, why such claims have been overemphasized under the fire of criticism that is sometimes stupid, and sometimes based on the assumption that the evolutionists claim a finality for the evolution theory of the kind that philosophers and theologians themselves affect. It is true, there have been philosophizers amongst biologists who, formulating laws of evolution, have given grounds for such reprisals, but I venture to think that they are the exceptions and not in the majority. Then, too, some of the popularizers of the theory of evolution have made exaggerated claims. They are picked out by their opponents not only as fair game, but, for purposes of criticism, held up as the highest and best exponents of the evolution doctrine. But there has always been a relatively large group of biologists, less vociferous perhaps, calling themselves evolutionists, who have tried to take a more moderate and even critical view of what the theory has done, and can do, for an understanding of the living world in and around us. Within their ranks, the theory has been constantly under review, realizing that it was a generalization rather than a verifiable conclusion. Since Darwin's time there has been a good deal of valuable criticism of the theory from biologists themselves; there has also been found much further evidence that has supported the theory; and above all it has come to be realized that the theory of evolution can be studied by the same methods that have been successful in other branches of science—that evolution is not so much a study of the history of the past, as it is an investigation of what is taking place at the present time.

DE VRIES'S MUTATION THEORY

The period immediately following Darwin—approximately thirty-five years—brought to light mainly the same kind of evidence to which Darwin appealed. The most obvious influence of the theory of evolution on biology led to the building up of imaginary pedigrees in the animal and plant kingdoms. Something was accomplished, but not much advance was made concerning the principles of evolution. Speculation became rampant, and only here and there were sporadic efforts carried out to get quantitative data on suitable material subjected to experimental control.

The formulation of the mutation theory in 1900 may be taken as the starting point for the study of evolution by more exact methods. Since then progress has been rapid and substantial.

While the modern study of the mutation process may be said to have begun with de Vries, its central idea was not entirely new, nor has its later development followed strictly the lines laid down by de Vries. De Vries himself states that he derived his theory in part from his earlier theoretical ideas in his book on *Intracellular Pangenesis.* Again, if we consider discontinuous variation as the most essential element in de Vries's theory, the idea had already been suggested and emphasized, especially by Bateson (1894), and later by Korschinsky (1899–1900). Galton still earlier (1889) had also appreciated the significance of discontinuity in variation as a possible source of evolution.

But it was not so much the idea that variation is a discontinuous process that makes de Vries's contribution significant. It was rather, as he thought, his detection of the process of mutation at work, and his demonstration that it is playing a rôle in the evolution of certain forms living today. Here, if de Vries was correct, was a chance to study by direct observation and controlled experiment the processes by which evolution of animals and plants comes about.

The sequel has, I think, largely justified the expectation. It is true that a good deal that de Vries recorded as the result of mutation has, during the last thirty years, come to have a more special interpretation, or rather several interpretations. Nevertheless, the later development has been a direct and continuous progress out of the materials and methods initiated by him. A few illustrations of de Vries's earlier work, and its expansion by himself and others, will serve to illustrate the progress that has taken place.

In 1886, de Vries found in a field near Amsterdam plants of the evening primrose, Oenothera lamarckiana (Fig. 1), growing wild. They were supposed to have escaped from cultivation, since this variety of evening primrose is not indigenous to Europe. Its progenitors had been introduced from the United States. Amongst these wild plants he discovered two new varieties, brevistylis and laevifolia. From a collection of the seeds of lamarckiana from the same locality he raised numerous plants through several generations. In a total of about 50,000 individuals he later obtained about 800 mutants that fell into seven mutant types, to which he gave the names nanella, lata, albida, gigas, oblonga, rubrinervis, and scintillans. Some of these bred true; others produced a greater or smaller number of types like lamarckiana. The same kind of results have since been obtained many times by others, and the original list of new mutants has been greatly extended.

Here, then, according to de Vries, is a plant which at the present time is producing a considerable percentage of new types in each generation—some of which breed true and may be called elementary species. Some of these new types vary from the original parent types in one or more striking differences; others are not very different—in fact, only a trained observer would see the differences. De Vries insisted from the beginning that the distinctive feature of mutant types is not the degree of departure from the original type, but the transmission of a whole new set of characters to their

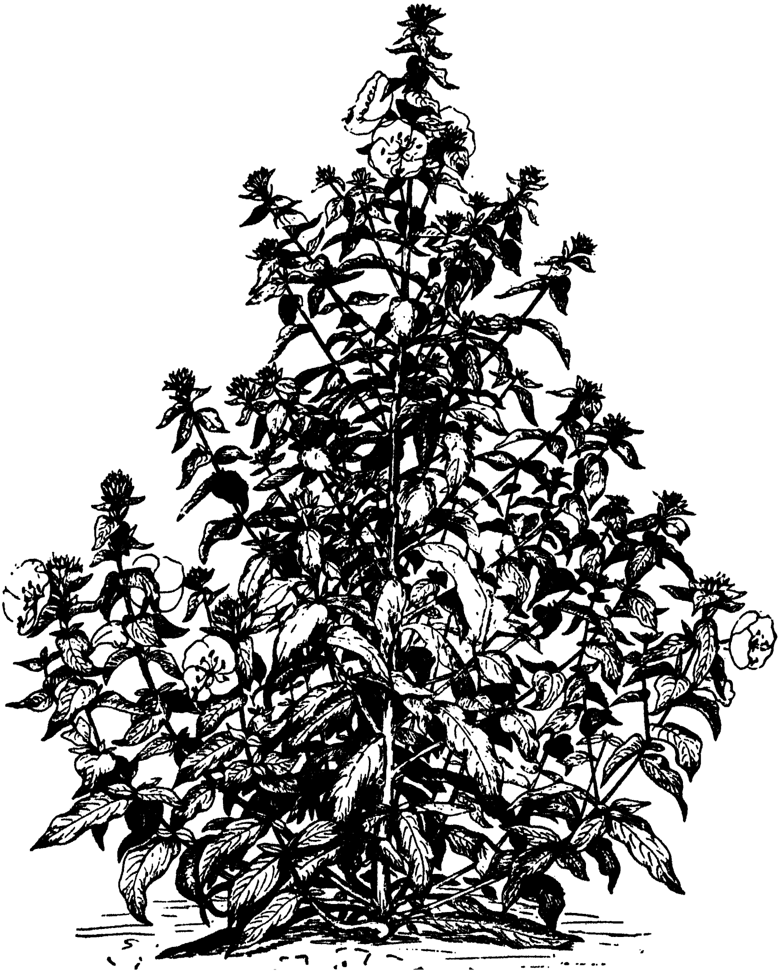

FIG. 1. *Lamarck's evening primrose* (*Oenothera lamarckiana*). (*After de Vries.*)

descendants. This consideration affirms that mutants differ from the original types in nearly all of their details. In some of the mutants the departure may be very apparent; in others it may be scarcely observable. He looked upon the mutant as a new creation, a new complex of characters. Nevertheless, de Vries argued that the mutation process that gives rise to a new elementary species * is itself the result of a single change in the germinal material of the parent.

It is not evident to us today that at this time de Vries had sufficient experimental evidence on which to base such far-reaching conclusions. As a result of Mendel's work, on the other hand, it has become generally recognized that changes in a single unit in the germ-plasm may produce changes identical with some, at least, of those discovered by de Vries. But it is also true that more than half of the early mutants of de Vries can no longer be claimed to result from single unit changes, unless one is prepared to accept any sort of change as a unit change. This will be made clearer when we come later to examine the rôle of the chromosomes in the mutation process.

Criticism of de Vries's interpretation was forthcoming along two obvious lines. Certain critics said that Oenothera lamarckiana is a garden hybrid, and that the observed mutation process is no more than a well-recognized property of hybrids to split into their component parts. Such an interpretation seemed to be supported by the fact that no wild species corresponding to lamarckiana could be found in America. This criticism has now been completely disposed of. If the mutation of Lamarck's primrose is due to the now familiar process of Mendelian splitting, we should expect

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* In recent years an important distinction has been made between elementary species (sometimes called *Jordanons*), which correspond in a general way in the wider terminology to varieties and races, and the species of Linnaeus (called *Linneons*) of systematic writers that are collective groups. Linnaean species in this sense would then be regarded as different from one another in a large number of differences, each of which would be like the single differences between elementary species.

to find evidence of this in the ratios that are characteristic of Mendelian inheritance. In fact, except for two or three of the original types, the ratios depart widely from such expectations.

A more significant answer to the hybrid theory is that other species of Oenothera, admittedly wild species, give similar mutational types.

A further argument, supposedly in favor of the hybrid condition of lamarckiana, was later advanced. It was pointed out that many of the pollen grains are abortive, and it has been claimed that this is a distinctive feature of hybrids. Here, again, the answer is that several wild species of Oenothera also have abortive pollen grains. Only by a fanatical insistence on the universality of this interpretation of abortive pollen grains could these other forms be claimed to be hybrids. Furthermore, the discovery of the occurrence of lethal genes has put this problem on an entirely new footing.

However, it is no longer necessary to depend on arguments of this general character. Recent work has put the whole matter in a different light—and in passing it may be pointed out that the new work has not come from these academic criticisms of de Vries's work, but from a study of the process of mutation itself by methods similar to those inaugurated by de Vries.

THE CHROMOSOMES

In order to make clear the kind of evidence on which the material basis of heredity rests, it will be necessary to consider certain information concerning the elements in the germ-cells, namely, the genes carried by the chromosomes.

The chromatin of the resting cell consists of a threadwork of material in the nucleus of the cell. When the cell is about to divide, the surrounding wall of the nucleus disappears. Its chromatin thread condenses into bodies called chromosomes, (Fig. 2a), that may have the shape of rods, or beads, or bent threads. A spindle-shaped structure (Fig. 2b) made up of fibres, develops near the chromosomes. At each pole of the spindle a star-like structure is often present (especially in animal cells) whose rays extend out into the protoplasm. The

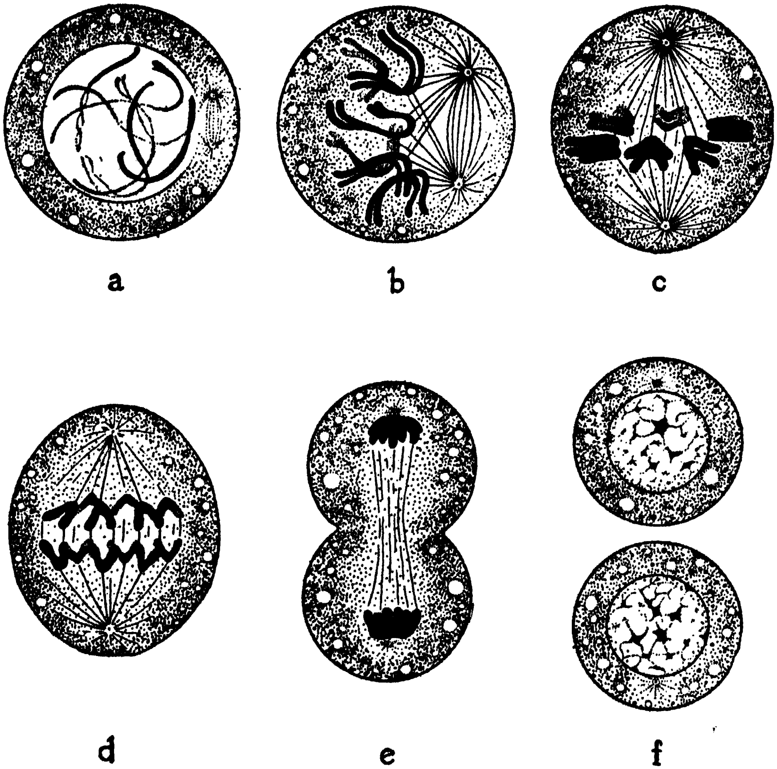

FIG. 2. *Diagram of ordinary cell-division, illustrating the lengthwise splitting of the chromosomes into equivalent daughter chromosomes. (Modified from Agar.)*

chromosomes become attached to the fibre-like lines at the equator of the spindle (Fig. 2c). About this time each chromosome can be seen to be split throughout its length, into exactly equal halves, or daughter chromosomes. These begin to migrate, (Fig. 2d), toward one or the other pole of the spindle. Each pole gets half of each original chromosome. The cell then constricts, (Fig. 2e), in the plane of the equator of the spindle, or, as in many plant cells, a partition forms at the equator. The constriction divides the cell into two. The chromosomes then pass into a resting nuclear stage (Fig. 2f).

Each animal or plant has a definite and characteristic number of chromosomes. The same group appears in all the cells of the body whenever the cells divide. In many species all the chromosomes have nearly the same shape; in other species they may have very different shapes.

The size of the chromosomes in different species varies, depending in part on the size of the cell (or nucleus) in which they are contained, but to a large extent their size in different species is not correlated with cell-size nor closely with the number of chromosomes in the cell. In Figure 3, the chromosomes of somatic cells of nine species of animals and plants are all drawn to the same scale. The chromosomes in the segmenting egg of the worm, Ascaris, are few (four) and very large, while those in the fly, Drosophila, (eight) are extremely small. In the pea and in Crepis the chromosomes are large and few, while in Datura and corn they are more numerous and smaller. In the grasshopper (Mecostethus) the chromosomes are numerous, twenty-three, and very large in comparison with those of Drosophila. In man the chromosomes are numerous, forty-eight, and relatively small. In all cases here figured the chromosomes are in the equatorial plate stage of cells about to divide. The differences in size

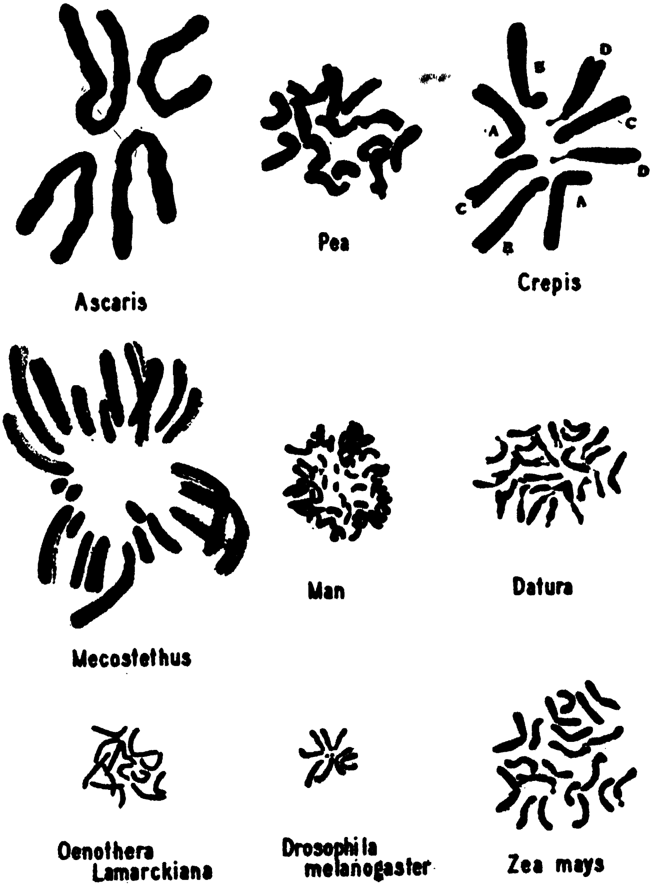

FIG. 3. *Chromosome groups (somatic and diploid groups) of nine species of animals and plants drawn to the same scale. All from equatorial plates.*

tell us nothing of the number of genes or their sizes in the different species.

There are two chromosomes of each kind in each cell. This relation holds not only for their visible form, but for their invisible structures as well. Part of the modern work of genetics is concerned with the invisible constituents of the chromosomes. These ultimate units of the chromosomes are the postulated units of genetics, the genes.

The only significant exception to the duplicate nature of the chromosome group is sometimes found in one pair of chromosomes concerned with sex-determination in those animals and plants with separate sexes. Here there may be an unequal pair, or one member of the pair may be absent in one sex. This difference, as will be pointed out later, furnishes the mechanism by which the two sexes are maintained in about equal numbers.

In hermaphroditic forms this differential pair of sex chromosomes is not present. Most (but not all) of the flowering plants, such as Oenothera lamarckiana, are hermaphroditic, hence for our present purpose the sex chromosome mechanism is not involved in what follows.

The constancy in the number of the chromosomes for each species is one of the significant facts that modern cytology has contributed to the cell-theory. Equally significant is the conclusion that the chromosomes retain their individuality through successive cell-divisions. This is interpreted today to mean that each chromosome is made up of a fixed number of units or genes that lie in linear order in each chromosome. There are hundreds of genes in each chromosome. Each gene is probably beyond the highest powers of our microscopes, but from rough calculations it seems probable that they are not smaller than the largest known organic molecules. These conclusions regarding the genes (their definite number, their arrangement, their constancy) are derived, not from direct observations, but from genetics, and furnish the basis of modern work on heredity.

What has just been said about chromosome numbers is the rule—the almost universal rule. But occasionally there are exceptions, and it is with these exceptions that some of the mutants of de Vries are concerned.

Occasionally a plant appears which has double the number of chromosomes. It is called a tetraploid or tetraplant. There are several ways in which tetraploid cells may arise. Tetraploidy is most often due to the failure of a cell to divide into two after the chromosomes divide. The descendants of such a cell continue forever to have the double number of chromosomes. One of de Vries's mutants, called gigas, was a tetraploid.

Occasionally, too, a plant with three sets of chromosomes appears. It is called a triploid. These also have been found amongst the mutants of the evening primrose, and can be produced by fertilizing a tetraploid with pollen from a normal or diploid plant.

A mutant that frequently appears has only one more chromosome than the normal. This may be called a heteroploid, or extra-chromosome type. Several of de Vries's mutants belonged to this group, and others have since been found.

The most complete study of extra-chromosome plants is that carried out by Blakeslee and his co-workers on the common jimson weed, or Datura stramonium. The diploid number of chromosomes is twenty-four, as shown in the diagram, (Fig. 4a). The triploid and tetraploid groups are also shown, (Fig. 4b, c). The heteroploid groups with extra chromosomes are represented in Figure 4d, e, f. Any one of the twelve chromosomes may appear in triplicate, each giving a slightly different kind of plant.

In addition there are other forms in which four of a given chromosome may be present (Fig. 4e), and still others in which two extra chromosomes belonging to different pairs may occur (Fig. 4f), etc. These new types furnish the geneticist with interesting materials for problems in heredity. It is doubtful whether such types could establish themselves as a rule in nature. In several respects, most of them are inferior to the wild type.

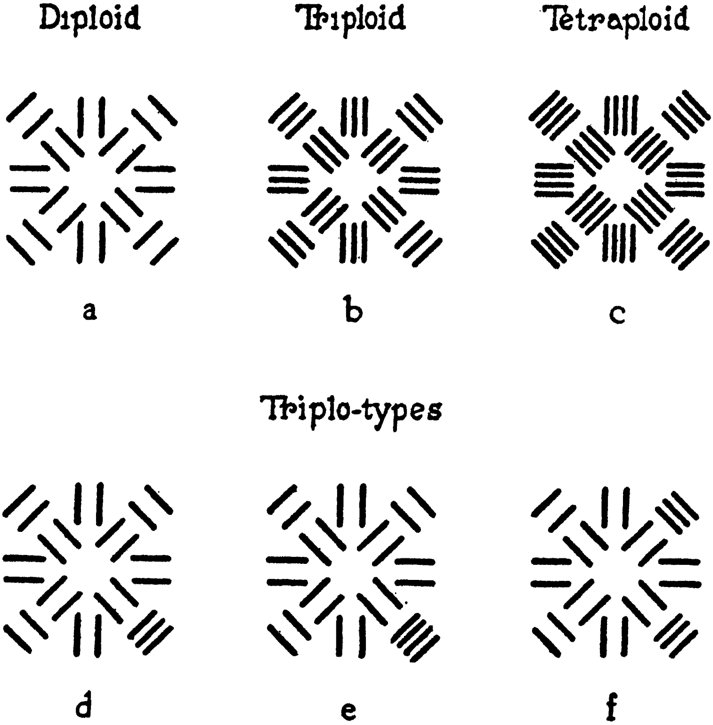

FIG. 4. *Diagram of chromosome numbers in Datura: above, diploid, triploid, tetraploid; below, extra-chromosome types.* (*After Blakeslee, from Journal of Heredity.*)

This last statement is less true for the tetraploid type and it seems not improbable that through this type and its resulting combinations new forms with a new number of chromosomes may sometimes establish themselves as new, elementary species. In support of this view another field of investigation must be considered. It has been found in many wild species, and also in some cultivated plants, that series of types exist that are characterized by being multiples of a basal number of chromosomes. Many such polyploids are known. A few of them may be mentioned here. In cultivated wheat there are diploid varieties with fourteen chromosomes (basal number, $n = 7$), tetraploid, and hexaploid varieties. Amongst wild and cultivated roses, with fourteen chromosomes ($n = 7$), there are threefold, four-, five-, six- and eightfold types (Fig. 5). Amongst chrysanthemums, maples, sedges, hawthorns, raspberries, strawberries, clover (Fig. 6) and several other genera, multiple chromosome forms have been described.

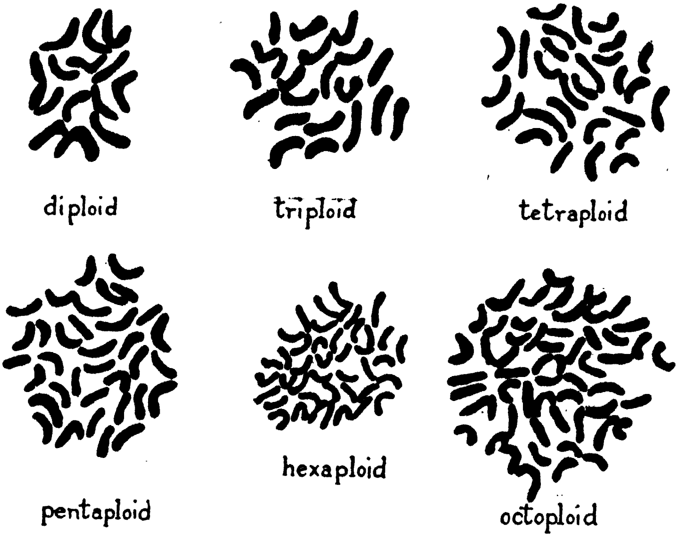

FIG. 5. *Diploid and polyploid groups of chromosomes in roses.* (*After Täckholm.*)

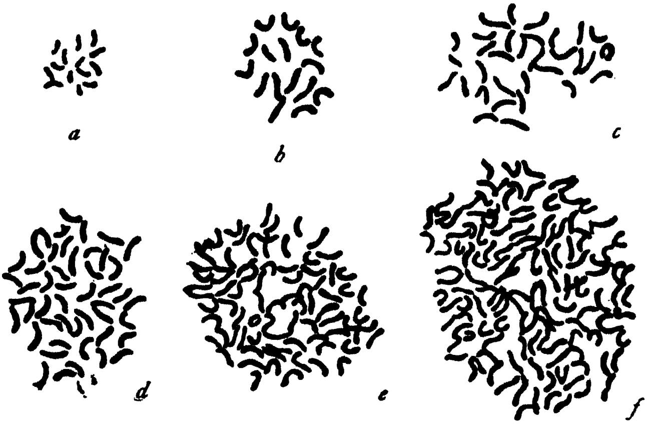

FIG. 6. *Diploid and polyploid groups of chromosomes in Trifolium. (After Karpechenko.)*

Two interesting cases have been found where, through the crossing of such forms, new stable combinations have been formed. In one of the cultivated poppies there is a race with fourteen chromosomes ($n = 7$, Fig. 7a) and another with seventy chromosomes ($n = 35$, Fig. 7c). Ljungdahl crossed these and produced a race with forty-two chromosomes, ($7 + 35$, Fig. 7b), that is stable and perpetuates itself. Here one of the original plants was double seven, the other ten times seven. In the hybrid (forty-two chromosomes) these combine as twenty-one pairs.

The second example involves a cross of two genera, a cabbage and a radish, Rhaphanus sativus by Brassica cleracea. This cross has been studied by Karpechenko. Each species has nine chromosomes. The bastard or hybrid has eighteen chromosomes (Fig. 8). When the germ-cells form, the two sets do not unite, and gametes with various numbers are formed. The vast majority of these are abortive, but amongst them there are a few ripe gametes with nine radish and

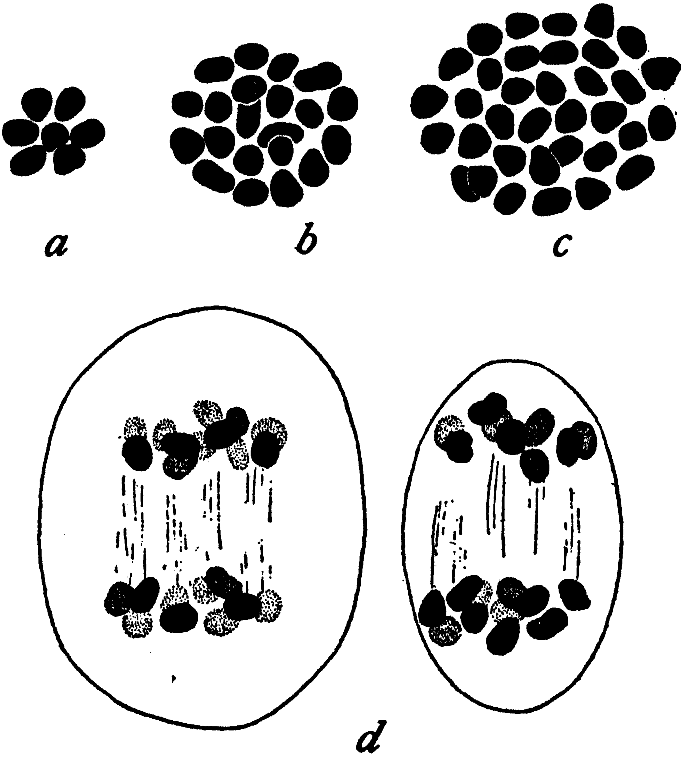

FIG. 7. *Cross between a poppy, a, with 14 chromosomes* ($n = 7$), *and one, c, with 70 chromosomes* ($n = 35$). *The hybrid, b, has 42 chromosomes* ($n = 21$). *In d the 21 chromosomes that have paired are separated and are moving to opposite poles in the maturation division.* (*After Ljungdahl.*)

nine cabbage chromosomes. These are functional and give new plants with thirty-six chromosomes. As an alternative, unreduced gametes would give the same result (see diagram). The hybrid is fertile and self-perpetuating. It is called Rhaphanobrassica (or radish-cabbage). A third bastard type was made by combining the last with another species, as shown to the right in Figure 8. Cases of this sort show how

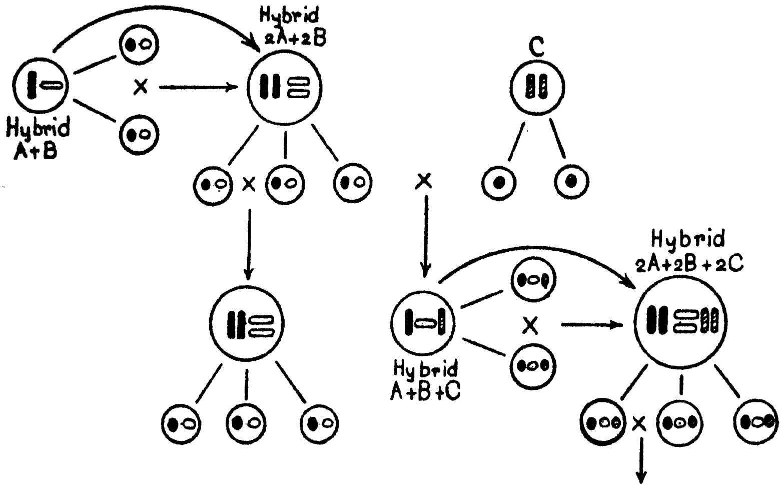

FIG. 8. *Diagram showing the combination of the chromosomes in a cross between radish and cabbage.* (*After Karpechenko.*)

new species may arise by crossing, and it is quite possible that even in nature such combinations have occurred.

GENE MUTATIONS

So far we have considered one kind of mutant change, or better, permutations in which whole chromosomes are involved. The main reason for taking up these first was that most of the de Vriesian mutants of Oenothera are of this kind. But we have come to associate the term mutation with a different kind of change, a change in only a single element in a chromosome. These are called point mutations or gene mutations.

These point mutations have been discovered in many animals and plants, both wild and under domestication. When we say that they have been *discovered,* certain reservations are necessary. Strictly speaking, a point mutation may be said to be known, as such, only when it has been traced to a definite locus in a known chromosome. In fact, while hundreds of cases are accepted as mutants of this kind, their accurate location has been determined in relatively few cases, notably in several species of Drosophila, in maize or Indian corn, and a few other animals and plants where approximate locations have been given. It is important to emphasize this fact, because there is no way of determining from the realized characters of a new type whether it is a point mutation or some other sort of chromosomal disturbance. If the new character should be the result of an environmental change or an abnormality in development, this can be demonstrated by breeding, i.e., by showing it to be not inherited. Some of these questions will come up again for discussion, but for the present it will suffice to keep in mind that the proof that a point mutation has occurred can be obtained only when it has been located in a known chromosome group. Nevertheless, in most cases where it has been shown that a variant differs from other members of the same race or species by a single hereditary factor, it is probable that the difference is due to one mutant change, and may be provisionally accepted as the result of a point mutation. Many such cases have been recorded.

For instance: Among domesticated animals and plants hundreds of types are accepted today as differing from one another by single hereditary differences—horses, cattle, sheep, pigs, rats, mice, guinea-pigs amongst animals; and wheat, rye, oats, sweet peas, garden peas, corn, tobacco, and a long list of other flowering plants.

In the vinegar fly, Drosophila, over five hundred mutants are known and new ones are continually appearing. Most of these have been definitely shown to be point mutants. The changes affect any or all parts of the body. A few examples of these mutants will show the great variety of characters affected. Drosophila furnishes excellent material to illustrate the mutational process, because nearly all of the mutants have come directly from pedigreed cultures of wild-types; hence their exact origin is known.

In Figure 9, eleven modifications of wing characters are represented, each having arisen in known stocks (Fig. 9a) by a single mutation-change. Some of the genes lie in the sex chromosomes (X), others in the second and third chromosomes, and one (Fig. 9-l) in the fourth. In Figure 10, five modifications of the bristles are shown, each of which has arisen from the wild-type (Fig. 10a) as a single mutation. In Figure 11, eight changes in the eye are represented. The normal or round eye is drawn in Figure 11a; the others, except Figure 11b which represents the white-eye, are structural changes. There are also many mutant eye-colors, probably forty or more.

In the mutants just described a gene has changed over to a new gene, but in an ever-increasing number of instances the same gene has produced more than one mutant type. These are called *multiple allelomorphs*. For example: in Drosophila there are at least eleven mutations at the locus of the white-eye (Fig. 11b),; cut wings (Fig. 9d) has at least ten mutants; vestigial wings (Fig. 9f) has at least eight mutants; forked bristles (Fig. 10f) six; scute (Fig. 40) fifteen to twenty types that can be separated. Each of these allelomorphs affects the same organ in much the same way, and when other or secondary effects are produced in other regions they are also as a rule found in the same organs in a given series of allelomorphs.

It is also interesting to note that in nature multiple allelo-

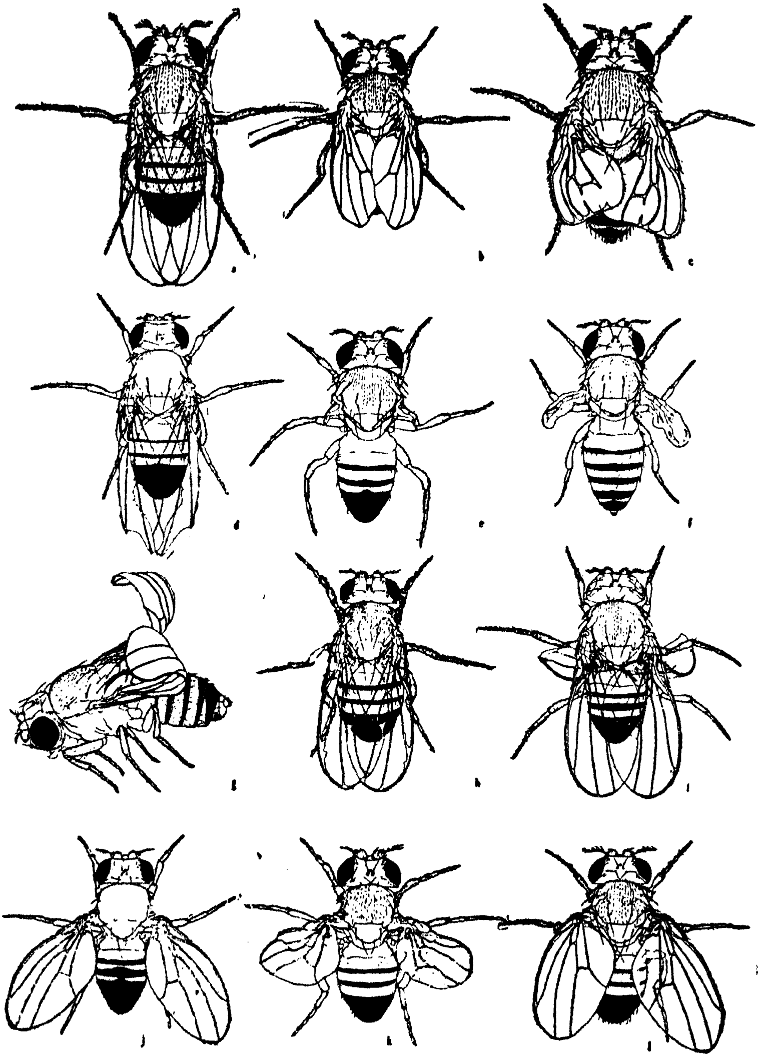

FIG. 9. *Eleven mutant wing characters of Drosophila melanogaster: wild-type, or normal male, Fig. 9a; Fig. 9b, miniature; c, rudimentary; d, cut and hairless; e, no-wing; f, vestigial; g, curly; h, delta; i, bi-thorax and glass-eye; j, dichaete; k, crumpled; l, bent.*

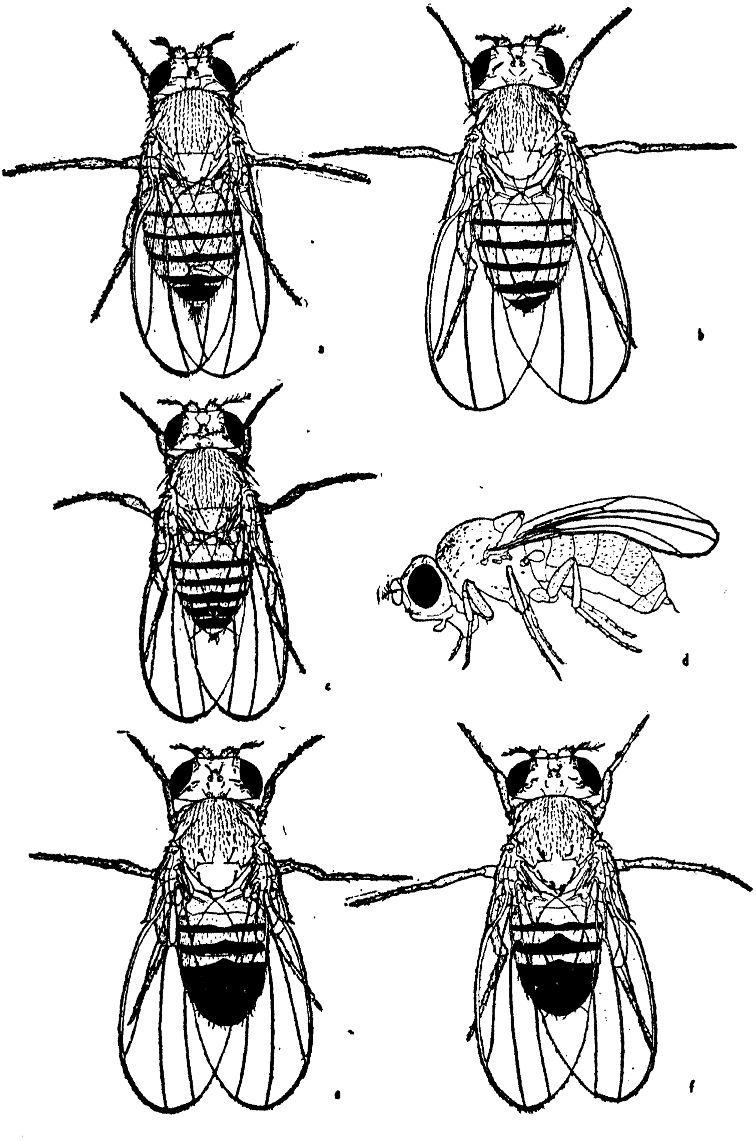

FIG. 10. *Five mutant bristle characters of Drosophila melanogaster: wild-type female, Fig. 10a; Fig. 10b, minute; c, hairy; d, shaven: e, stubble; f, forked. (See also Fig. 9d, hairless, and Fig. 9j, dichaete.)*

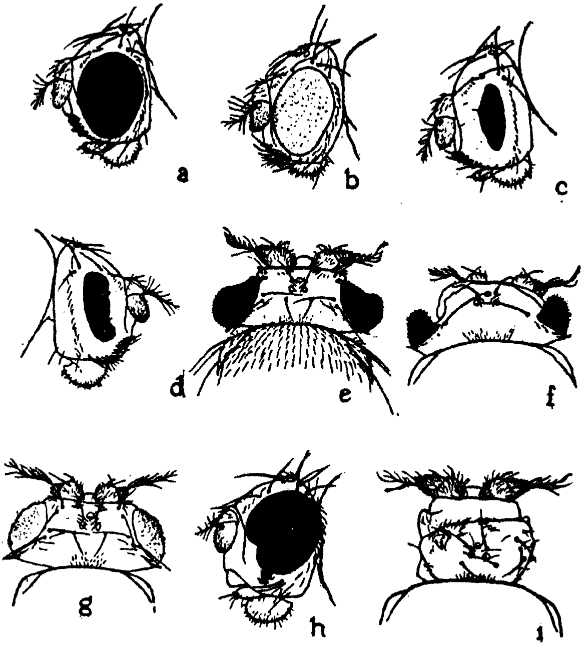

Fig. 11. *Eight mutant eye-characters of Drosophila melanogaster: wild-type eye (side view), Fig. 11a; Fig. 11b, white; c, Bar; d, infra bar; e, deformed; f, Lobe; g, rough; h, kidney; i, eyeless. (See also Fig. 9i, glass.)*

morphic varieties have been found. Zulueta has described several such types in the beetle (Fig. 12) Phytodecta variabilis, from Spain. Other such series are known in this group. Nabours has reported a series of such forms (thirteen in all) in the ground locust, Paratettix texanus. Eight such types are known in the snapdragon (Antirrhinum). In one of the aquarium fish from Central and South America, Lebistes reticulatus, a series of males is known that differ from one another in certain color characteristics. These may be allelomorphs, or possibly permutations of whole chromosomes.

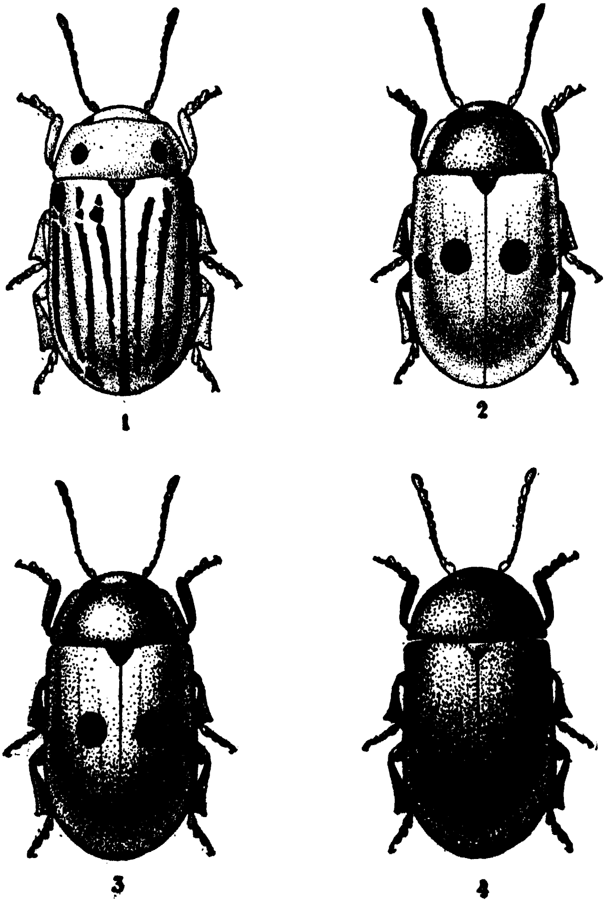

Fig. 12. *Four varieties of wild beetles whose differences are due to allelomorphic genes. (After Zulueta.)*

In some of the others, there is a suspicion that whole chromosomes may be involved rather than point mutations, and, if so, these cannot be at present referred with certainty to the category of point mutations. The main fact remains, however, that in nature the same kinds of changes are found that are more familiar in pedigree cultures, and some of these mutant types have established themselves as characteristic of wild-types or varieties.

SOME GENERAL FEATURES OF POINT MUTATIONS

There are certain general features concerning mutation that have a bearing on the relation of this process to the theory of evolution. In the period immediately following the discussion of Mendel's paper, too much emphasis was placed on *dominant* and *recessive* characters. This was due in part to the rather sharp distinction that Mendel had made between the members of a contrasted pair of genes which we now call allelomorphic genes. Thus, yellow color in the seed of garden peas dominates green. This means that when a variety having yellow seeds is crossed to a variety having green seeds, the seeds of the offspring are yellow, which is said, therefore, to dominate green. This sort of relation held for all the seven pairs of characters that Mendel discussed. Similar relations have been found for other pairs of allelomorphic characters. But in many other cases the character of the hybrid is intermediate between the characters of the parents. Thus when a white-flowered four o'clock is crossed to a red-flowered type the offspring are pink. In fact, when the whole field of known cases is looked over, one is impressed rather by the intermediate character of the hybrid offspring than by the complete dominance of one character over the other. This does not mean that the characters of the hybrids are strictly intermediate; they may in fact be more like one parent but still show some influence of the other parent.

For our present purposes there is another relation that is very important when the mutational process is used in connection with the theory of evolution. This is the relation of the characters of the original (wild) type, from which the new mutants arise, and the corresponding allelomorphic characters of the mutant. In many cases, but by no means in all, the new characters are *recessive* more or less with respect to the wild-type—the recessiveness may be, and often is, only partial, so that the hybrid shows characteristics of both of its parents. This relation involves an important fact when we come to consider the possible rôle of mutation in evolution, and will be discussed more fully in the next chapter.

THE ABNORMAL CHARACTER OF MANY MUTANT TYPES

Another characteristic of new mutant types that has given rise to a good deal of discussion is their defective or abnormal character. By defective or abnormal we mean generally that the presence of a new character or characters makes the individual less likely to survive under the conditions of life to which the original type is already adapted. Sometimes this means that the animal or plant is deficient in some one character that is advantageous to it in its general relation to the environment. In other cases the mutant may be less vigorous or produce fewer offspring than its prototype, which is a disadvantage. Only under the artificial conditions which man can supply can such types persist for any length of time.

Here two considerations must be kept in mind. First, wild animals and plants are found structurally specialized to a particular complex of environmental conditions. They are, to the evolutionist, the end-product—the perfected product of the test of survival. Any sudden and considerable change in the structure of such an individual is likely to be deleterious.

Second, we should expect that any improvement would be along physiological lines such as greater vigor, or resistance to cold or to heat, or greater strength, or better functioning of one or another organ. Characters of this sort are difficult to detect and are seldom reported by geneticists. However, it is known that they do occur. Perhaps the best illustration is found in resistance to certain diseases. For example, at times individuals are found that are more than others resistant to the attacks of certain diseases. It is known that some of these characteristics are inherited, and in a few cases there is evidence that they are the product of specific genes. It is the occurrence of such mutant characters that encourages us in an attempt to apply the evidence from mutation to the theory of evolution. Their occurrence reassures us that the mutation process may furnish significant evidences for evolution.

It need not be concluded from what has just been said that the ordinary mutant types have no value in biological theory or practice. They furnish abundant materials for the study of heredity. The fundamental laws of inheritance can be studied as well by utilizing such mutant characters as would be the case were they characters useful to the individual. Moreover, a great number of mutant types furnish mankind with the materials for artificial breeding. Not only do fantastic types of animals and plants produce varieties that are highly prized for their bizarre or aesthetic interest, but there are numberless characters of domestic animals and plants, depending on gene mutations, that have great economic value. Their discovery and maintenance is in itself an evolutionary process; and even if plant and animal breeding often makes use of characteristics that, without human protection, would perish, it is, nevertheless, a real evolution that is taking place. Whether it is fair to use this argument for evolution at large may be disputed. Some of the factors involved may be different in the two cases; nevertheless the demonstration that a process of evolution may take place in which all the other factors, except man's selection and protecting agency, are present, cannot be disregarded if we take a broad and generous view of evolution.

In the human race many aberrant characters have been described that are inherited. Their perpetuation has a bearing on the chances of survival of the race, especially when, as in the more civilized countries, the preservation of all individuals that are born has a profound emotional and even an ethical significance. To what extent the preservation of weaker types, that could not compete successfully under "natural conditions" in a physical sense with the original or aboriginal forms, is desirable, raises many complex and difficult problems for the future of mankind. What may seem to the savage to be a weaker physical type may, under the conditions of a highly specialized social group, be a variant that has more value to the group as a whole than the original type from which the new mutant has arisen. In our most highly valued domesticated animals and cultivated plants there are many examples of new valuable mutant types that can only survive with the assistance of the protection and care of man. It is not improbable that the evolution of the human race will in the future also be carried on under man's direction. If so, one important function of the science of genetics is to see to it that this is not done stupidly and without foresight.

CHAPTER II

THE CELLULAR BASIS OF HEREDITY AND EVOLUTION

It was pointed out in the preceding chapter that without a knowledge of what was taking place in the chromosomes, the mutation process in the evening primrose would have been difficult to interpret. It may now be stated that the chromosomes not only furnish a physical basis for the interpretation of Mendel's theory, but also account for a great many of the more complex phenomena which geneticists discovered later. The interpretation of these discoveries would have been seriously hampered without an understanding of the chromosome mechanism.

As already stated, the number of chromosomes is known to be constant for each species of animal and plant. The size and shape of the chromosomes are also as constant and characteristic as is their number. There are two of each kind of chromosome in each cell, one of which has come from the mother and one from the father. The members of each pair are alike in size except for one combination of sex-chromosomes, in which the members may differ in size and shape, or one member of the pair may be absent in one sex.

It is important to repeat once more that all the cells of the body have the same chromosome group. It follows that the differentiation of the cells of the body is not due to visible changes in the chromosomes or in their number, no matter how different the functions of specialized body-cells may be. It has also been practically demonstrated that all of the genes are present in every cell, regardless of its specialization.

The continuity of the chromosomes is insured by the process of cell-division. When a cell divides, whether body-cell or primordial germ-cell, each chromosome splits throughout its length into exactly equal halves, and the halves move to opposite sides of the dividing cell (Fig. 2). Each daughter cell receives half of each of the original chromosomes. In this way the chromosomes are transmitted from one cell-generation to the next, and the number is kept constant. It might appear, if this went on indefinitely without any compensating process, that the chromatin material would finally be so attenuated that it would practically disappear. In fact, however, the daughter chromosomes do not become subdivided into infinitely thin threads, but each increases in size before the next division. Whether this growth takes place at the time of splitting, or after the halves have moved apart, is not certainly known at present. There can be no doubt, however, that the daughter chromosomes as a rule increase again to their former typical size before the next division.

If we think of the genes as material particles, or treat them as such, we must suppose that when the chromosomes divide each gene is divided into equal halves; and since, as the evidence shows, the genes lie in a line within the chromosome thread, the gene also must have the property of growing to the original size at the time of or after each cell-division.

What happens to the chromosomes during the interval between cell-divisions, during the time that the cell is carrying on its specific functions, is not known. After each division, as the new nucleus in each daughter-cell is re-formed around the chromosomes, the chromosomes send out lateral branches that seem to form a network throughout the nuclear sap, or sometimes on the nuclear wall. Whether these branches ever actually fuse to form a network, or whether each remains contained within a little sac of its own, we do not know. But the fact that, when they reappear in sister-cells, sister-chromosomes lie in the same positions, suggests very strongly that they have retained their identity throughout the resting stages. This conclusion is consistent with the abundant evidence derived from genetics to the effect that the essential structure of the chromosome remains unaltered.

THE CELL-PLASM AND THE CHROMOSOMES

The chromosomes have come to be looked upon as the sole bearers of the hereditary characters. In volume they occupy a relatively small part of the cell. The rest of the cell, the part outside the nucleus, is spoken of as the cytoplasm, or cell-plasm, and sometimes as the protoplasm, although the latter is an older and less precise term that includes all the semi-fluid interior of the cell. Since the differentiation of the cell appears in the cytoplasm, and since it is this differentiation that gives the characters of the individual, the question arises as to how the chromosomes determine the direction of this differentiation. There has been much speculation concerning the way in which the chromosomes control the cell-plasm, but at present nothing definite is known. De Vries long ago suggested in his theory of intracellular pangenesis that the chromosomes give off specific living units, i.e., units that have the power of self-multiplication, and that these bring about in some unknown way the reorganization of the cell-plasm. Others have suggested that the chromosomes give off enzymes, which, acting as catalysts, determine the differentiation of the cell.

On the other hand, students of embryology have brought forward definite evidence that the early development of the egg is determined by the organization of the cell-plasm. By organization is meant, in its simplest terms, no more than that the cell-plasm is not homogeneous but contains several regions having a definite relation to each other. During the early divisions of the egg these materials are distributed to different regions and into the resulting cells. It has also been shown that the early differentiation of these cells is related to their future development. In a rather crude sense these materials have been looked upon as organ-forming substances, but it is equally possible that, in a strict sense, they may not act so directly, but may rather determine the development of the cell by the relative amounts present in different cells, and by the physiological interaction of the cells on each other. However this may be, there is genetic evidence pointing clearly to the fact that many of the fundamental properties of the early development belong to the cell-plasm at the time when the egg begins to divide. An excellent illustration of this is shown by experiments of Boycott and Diver on the right or left symmetry of the shells of certain fresh-water snails. Sturtevant has pointed out that these results can be interpreted to mean that the hereditary symmetry of the body is determined by the cell-plasm. The same evidence shows, however, that this property of the cell-plasm of the egg is under the control of the chromosomes which have already influenced the cell-plasm in this way in earlier stages before the egg has reached its full development.

The question still remains whether the cell-plasm has properties of its own that are independent of the influences the chromosomes exert on it. There is experimental evidence bearing on this point which is positive as far as it goes. When reciprocal crosses are possible between two varieties or even species, the reciprocal hybrids are, as a rule, identical in their adult characteristics. This evidence indicates that the differences between the two varieties or species are determined by the dominant genes of the chromosomes and not by the cell-plasm. The conclusion must be accepted with caution, however, because it may be claimed that reciprocal crossing is possible, when it occurs, only because the cell-plasms are nearly similar for all characters common to the two varieties. The converse statement may bring out the point more clearly. It is possible that forms more widely different may possess cell-plasms so different in constitution that the chromosomes of the one cannot change over the cell-plasm of the other. There is no *a priori* reason why this may not be true. At present it is difficult, perhaps impossible, to settle the question by direct experiment; for, if the chromosomes of one species cannot normally develop in the cytoplasm of the other species in the early development of the egg, it is then not possible to determine whether or not in time, i.e., if the adult stages were reached, the cytoplasm could be changed over by the foreign chromosomes. There are, in fact, many cases known, when two widely different species are crossed, where the chromosomes of one species cannot properly carry out their normal divisions and distribution in the cell-plasm of the other species.

There remains one other category of cases to be considered in which there is direct evidence that there are present, in the cell-plasm, self-perpetuating units which are inherited, and which determine certain characters of the individual quite independently of nuclear influence. For instance, the plastids of green plants that become chlorophyll grains are present in the cytoplasm of the egg-cell. Such plastids may be absent in the pollen tube, hence the green-colored chlorophyll is inherited only through the cytoplasm of the egg. In other cases, however, both the egg and the pollen may contribute such plastids. Conversely, it has been suggested that the centrosomes, around which the spindle fibres develop when the cell divides, are brought into the egg by the spermatozoön, while those present in the egg when the polar bodies are given off disappear. In a case of this sort the transmission is through the sperm. This conclusion is offset to some extent by the fact that the egg can be made to develop by treatment with chemical reagents (without the entrance of a spermatozoön); hence it is evident that the egg can itself develop the mechanism for cell-division, provided an artificial stimulus is applied.

MATURATION OF THE GERM-CELLS

There is one extraordinary exception to the ordinary behavior of the chromosomes that is found at the time of ripening of the germ-cells, and at no other time. As the changes that take place at this time involve an important question for genetics, it is necessary to consider what transpires in some detail. In order to do so, we shall have to start at a time when the mass of germ-cells ceases to multiply by ordinary mitotic divisions, and the cells enter into new phases, the so-called maturation stages. The end-result of these stages is to reduce the number of chromosomes in each egg-cell, and in each sperm-cell, to half the typical number. We might say that this is the purpose of the maturation process, but to do so would expose us to the unnecessary criticism that we are pretending to explain something by ascribing a purpose to the process. The mechanism that accomplishes this result does something even more significant than halving the number of chromosomes; for, not only are they reduced to half their original number, but one member of each pair is sorted out to each cell—each germ-cell gets one of each kind of chromosome.

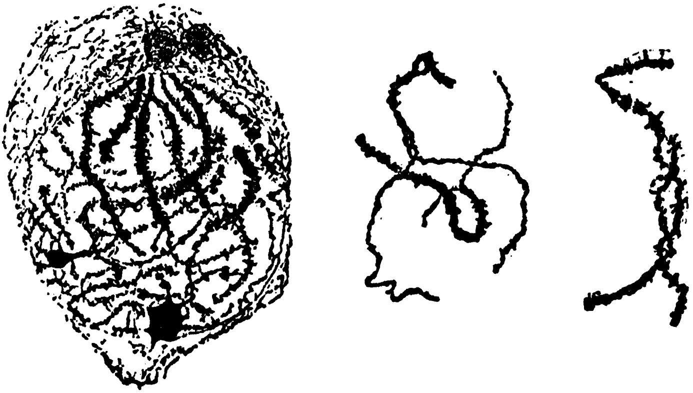

FIG. 13. *Conjugation of chromosome pairs at the time of maturation (meiosis) of the germ-cells of Batracoseps. (After Janssens.)*

This separation of the chromosomes is preceded by a striking phenomenon that never occurs at any other time in the life of the cells. The chromosomes come together in pairs, like mating with like (Fig. 13). Just before coming together, each chromosome has stretched out into a thin thread. The threads begin to come together in pairs at the free ends. If the two members of a pair are straight rods, the union probably begins at only one end. But many chromosomes are bent, having the form of a U, i.e., they are horseshoe-shaped, or even V-shaped. These begin to unite at both free ends, and come to lie side by side throughout their length (Fig. 14a).

They shorten as they do so. At this time it often looks as though they overlap here and there, or may be said to twist about each other. This condition is very difficult to interpret, and there is much difference of opinion in regard to what takes place. It should be stated that this overlapping cannot be seen in the living cells—at least, the details are invisible—which makes it somewhat difficult to get a correct picture of what is going on. Nevertheless, that overlapping, and even twisting, does take place is very probable judging from preserved and stained sections of the germ-cells. It would be even more important could we determine objectively whether, when the threads cross, they sometimes break at the nodal points and reunite in such a way that there is an interchange of equivalent parts. The cytological evidence fails to establish convincingly this relation, because the difficulties of interpretation of the preserved material are too great; but the evidence that genetics brings to bear on the point is so definite and convincing that a failure to appreciate it would be to reject some of the clearest results that modern genetic work has brought to light. The process is called *crossing over* —meaning interchange of equivalent blocks or pieces of homologous chromosomes. This genetic evidence will be considered later, but it may be stated here that the process brings about a re-combination of genes of two sister linkage-groups that is accomplished in no other way.

Despite the abundant genetic evidence that large sections of the chromosomes are involved when crossing over takes place, the actual demonstration that such an exchange has occurred has only recently been made by McClintock (in corn) and by Stern (in Drosophila). This was made possible by the discovery of material of such a kind that the genetic chromosomes were marked by known genes and the actual chromosomes involved were identified by special configurations (due to translocations, etc.). This evidence shows convincingly that where crossing over is involved, i.e., when a certain kind of individual is produced, the postulated chromosome exchange can be demonstrated cytologically.

Leaving this question aside for the moment, the later behavior of the pairs of united chromosomes may be described. As stated, they shorten during and after this union. The nuclear wall now disappears; a spindle develops from whose poles extensive rays extend out into the cell-protoplasm. The chromosomes move onto the equator of the spindle (Fig. 14b). The members of each pair separate—one member of each pair going to one pole, and the other member to the opposite pole (Fig. 14c, d). The cell then divides into daughter-cells, each with a single set of chromosomes, i.e., with one of each kind.

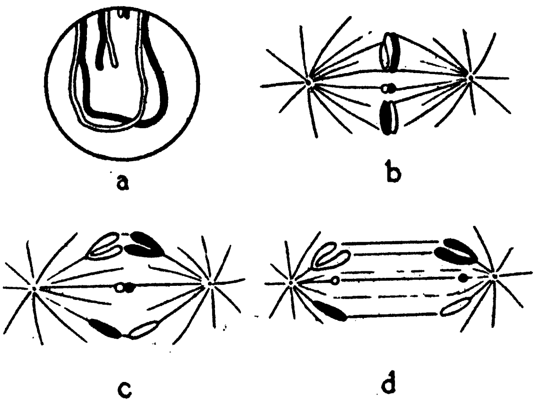

FIG. 14. *Diagram illustrating the conjugation and separation (reduction) of the pairs of chromosomes.*

It may be recalled here that before maturation of the germcells, when the full or double number of chromosomes is present, half have come from the father and half from the mother. When the maturation division just described takes place, the pairs of chromosomes that lie on the equator are placed at random with respect to the maternal and paternal components. Consequently, when the separation takes place, some paternally derived chromosomes pass to one pole and some to the opposite pole. In other words, only rarely would all the paternally derived chromosomes pass to one pole, and all the maternally derived to the other. In the resulting cells there are therefore all possible combinations of maternal and paternal chromosomes, there being in each, however, only one chromosome of a given kind.

Immediately following this first maturation division a second division takes place. This resembles an ordinary cell-division so far as the chromosomes are concerned. Each chromosome divides into like halves—splitting throughout its length, and half of each goes to one or the other pole. It is to be noted that this division does not further reduce the number of chromosomes in the daughter-cells, since each chromosome splits lengthwise as in ordinary divisions. It seems a superfluous division from this viewpoint, but may be an essential part of the mechanism of the division of the cell. By this I mean that each chromosome of the pair may be already split, or is about to split as in ordinary division, hence a second cell-division is necessary if the number of chromosomes is to be kept reduced to one-half the total number.

This account of the maturation divisions covers the essential facts, both for the ripening of the eggs and for the sperm-cells of animals. There are, however, some secondary differences in the two cases. The maturation of the sperm-cells (Fig. 15a–i) follows almost exactly the general scheme outlined above. Four cells with the reduced number of chromo-

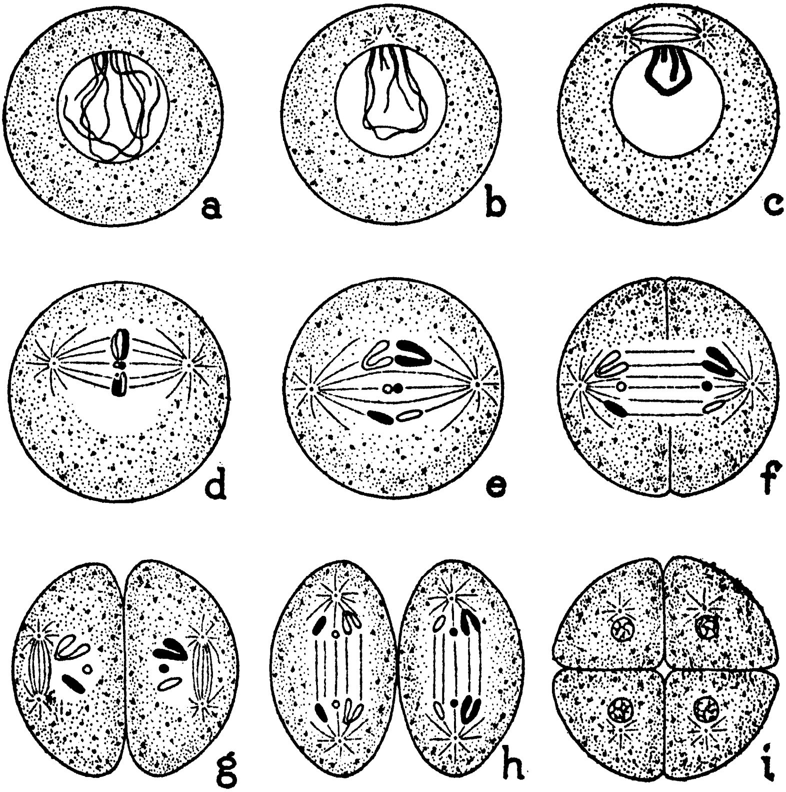

FIG. 15. *Diagram illustrating the conjugation and two following divisions in the maturation of sperm-cells.*

somes are produced from each sperm mother-cell. In plants, also, the maturation of the pollen is essentially the same as in animals, although there is a later division as the pollen tube penetrates the pistil. In the eggs of animals, on the other hand, the two maturation divisions, while essentially the same as in the sperm-cell, lead to the formation of one functional cell which we call the ripe egg and three functionless polar bodies (Fig. 16a–f). In the egg, after the conjugation of the chromosomes (in meiosis) has taken place and the chromosomes have passed to the spindle, the latter moves to the pole of the egg (Fig. 16a). There the paired chromosomes separate, moving to opposite poles, and a very small protrusion of protoplasm arises from the surface of the egg (Fig. 16b). The outer group of chromosomes passes into this protrusion, which then cuts off from the egg as the first polar body (Fig. 16c).

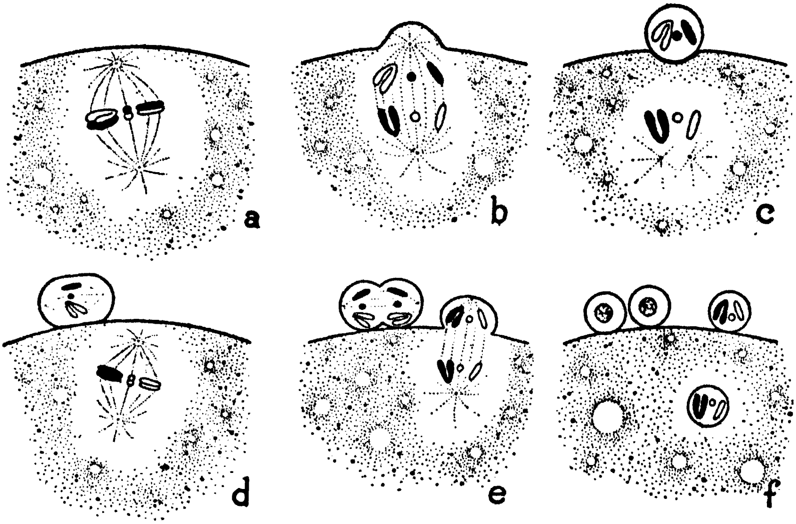

FIG. 16. *Diagram illustrating the two maturation divisions of the egg. Two polar bodies are given off.*

The inner group of chromosomes now passes to the equator of a new spindle that develops, which in turn orients to the pole (Fig. 16d). The chromosomes split lengthwise and pass to opposite poles. The outer group enters a second protrusion which becomes cut off as the second polar body (Fig. 16e). The inner group containing the reduced number of chromosomes now becomes a resting nucleus that retreats to the interior of the egg. Meanwhile the first polar body has divided (Fig. 16f). The three polar bodies and the egg correspond to the four sperm-cells, but only the egg is functional; the three polar bodies take no part in its further development.*

After, or even before, the maturation stages, the germ-cells undergo further changes. In fact, each becomes a highly specialized cell. The egg-cell has accumulated yolk before the polar bodies are formed, and has manufactured other materials essential to its development into an embryo. The sperm-cell becomes a motile cell, the nucleus condensing into the head, the protoplasm becoming a vibratile tail.

When a spermatozoön enters the egg its head absorbs fluid and becomes the sperm-nucleus (Fig. 17). The egg-nucleus also enlarges. The two come together and fuse into a single nucleus (Fig. 17c–d). The full complement of chromosomes is restored by this union. A spindle develops, the chromosomes of both sets pass to its equator. Each splits, the halves move to the poles, and the egg divides to form the first two cells of the embryo.

POINT MUTATION AS LOSSES OF GENES

Aside from the increase or decrease in the number of chromosomes described in the last chapter, Muller, and later others, have reported the occurrence of mutants after treatment with X-rays, that correspond in every way to the type

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* In order to simplify the account, the separation of the paired chromosomes is described as taking place at the first maturation division. There is some evidence that this does often take place, but the members of one pair or of all the pairs of chromosomes may sometimes separate at the second division. The end-result is the same. The account has been further simplified by ignoring the fact that the conjugating chromosomes may split lengthwise before the first maturation division so that four strands are present at this time instead of two. This condition may involve certain significant relations in crossing over; but for present purposes the results would be about the same if the chromosomes had not been "precociously" split.

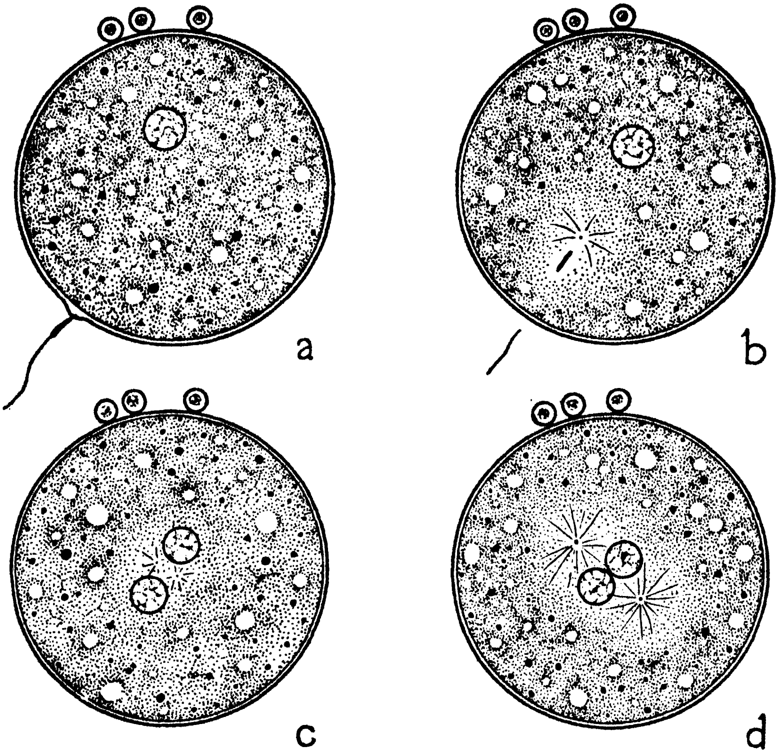


FIG. 17. *Diagram illustrating the fertilization of the egg and the formation of the two pronuclei and their union.*

of "spontaneous" mutation which is referred to as the result of a change in a single gene. Their occurrence raises a question that has been before geneticists for twenty-five years, namely: as to whether or not our familiar recessive mutations are due to losses of genes. The presence-and-absence theory of Bateson and Punnett (1905) rested on this assumption.

It might be argued that, if the breaking up of the chromosomes after treatment with X-rays is the result of an injury to them, point mutations may be the result of a smaller injury or loss to one spot or locus of a chromosome. The answer here is the same that has been advanced many times before in regard to all point mutations, especially recessive ones. An ever-increasing number of cases has shown that occasionally a recessive gene reverts to normal. The genes for scute and forked bristles in Drosophila sometimes behave in this way. In the light of what we know about genes it seems highly improbable that they can be manufactured *de novo,* or that a lost one can be replaced—a particular missing one. It has been reported on several occasions that, after treatment with X-rays, reversion to normal also takes place (Muller, Patterson, Timofeëff-Ressovsky), and it may be significant, too, that several of these cases are the same cases where reversion occurs without treatment. Patterson and Muller record eight mutations from non-forked to forked and seven from forked to non-forked. Scute has given similar results. As I have said, a few cases of this sort are known which may seem to nullify the argument that recessive mutants are due to the loss of genes.

But if these few cases of the sporadic return to normal seem inadequate to prove that all point mutations are not losses, it may well be that some point mutations are real losses. Evolution itself has sometimes been downhill—i.e., towards simplification. Many parasitic animals and plants furnish abundant evidence of loss of complexity in comparison with their relatives. The absence of wings in some insects, the loss of legs in whales, and many other changes of this kind are known. Disregarding the fallacy of arguing from character to gene, it might be assumed that such large losses are sometimes connected with the degradation of certain genes. In fact, most geneticists are ready to admit that genes may be lost at times, and there are several instances known where this may have occurred. From still another point of view it may be argued, since there is demonstrable evidence that pieces of chromosomes are lost or translocated, that it may well happen that individual genes drop out at times.

It is, however, the building up of new and more complex types that we usually think of in connection with evolution. Can we, then, give a theoretical account of how such constructive changes may have come about through changes in genes? Placing the argument squarely on the basis of chemical changes in the genes, we may assume that there may occur at times new molecular combinations that give new compounds, in a chemical sense. The chemical processes that go on during the growth of the genes, and the physical processes that occur when each divides, would appear to be molecular phenomena depending on internal relations that are more subtle than the gross effects we can produce by the application of extreme environmental agents, such as heat or cold or electricity or X-rays—agents deliberately chosen at the extreme points where they are known to give injurious or nearly fatal results. In this connection it is interesting to note that Muller and Mott-Smith have shown that the amount of radiation in the earth is inadequate to account for the ordinary process of mutation in Drosophila.

We know very little at present about the conditions under which the protein compounds of the body are built up, but we do know that they are synthetically reconstructed in the body, and to a limited extent in the laboratory. While for the present we must be content to rest the case for constructive changes in the germinal materials on such general arguments, it is worth while to realize that we are not going beyond the possibilities of chemistry and physics in pinning our hopes to future developments along these lines.

There is one further point in this connection that I should like to refer to, although I realize that it carries us perilously near to ultra-naturalistic considerations.

Are we justified in concluding that these postulated constructive changes in the gene are random changes on the ground that the end-products which they produce—the genetic variations—seem to be in all directions, or at random, as we say?

Such an inference would be a mistake, in my opinion, because the constructive processes in the gene, to which I have appealed, are dependent in the last analysis on the physico-chemical constitution of the gene itself. If so, we should expect that the building up of new genes would not be a random process at all, however rarely it may occur, but would be restricted by the composition of the original gene from which the new gene has come.

It is true that the possible number of new combinations in a complex organic molecule is very great, but still limited, and it is from this limited number of possibilities that the constructive material of evolution would come. If we had the complete ancestry of any one animal or plant living today, we should expect to find a series of forms, differing at each step by a single mutant change in one or another of the genes, and each a better-adapted, or a differently-adapted form, from the preceding one. This picture, disregarding the mutant changes that have been failures, may seem, at first sight, to imply that each progressive step was due to a corresponding advance in the same gene. Such a conclusion would be entirely unjustifiable from the evidence at hand. In the light of our present knowledge concerning mutation, inadequate though it be, it seems that the progressive steps occur in a change now in this gene, now in that. Large numbers of genes appear to be contributory to the evolutionary advances. This inference presents again the pictures of random changes in the genes, rather than progressive change in any one gene. It is only the end-stages that have survived that give the impression of a straight line of advance (orthogenesis). Nevertheless, such a view of gene changes is still compatible with the assumption that a building-up in complexity of the genes, taken as a whole, has occurred during evolution, and that these changes are limited in each case to the restricted possibilities of each gene. Put in another way, it may be said that by directing attention to the series of ancestral stages that have occurred, there may appear to be a relation between the properties of the genes and the adaptiveness of the resulting individual; but this would give a very erroneous idea as to what actually takes place during evolutionary progress, since it ignores the many false steps or failures to produce viable forms which experience shows are far more numerous than the successes. The latter consideration removes the teleological implication that there is a purposeful response of the gene to the adaptiveness of the resulting change in the organism.

CHAPTER III

MENDELIAN INHERITANCE AND ITS RELATION TO THE DISTRIBUTION OF THE GENES

GREGOR MENDEL'S now famous paper appeared in an out-of-the-way journal—that of The Natural History Society of Brünn. This journal had, however, a fairly wide circulation for the time, and the paper was no doubt seen by Mendel's contemporaries—in fact, there is on record his correspondence with a botanist of recognized standing, Nägeli of Munich. Nägeli failed to appreciate the significance of Mendel's discoveries, and his indifference may be taken as symptomatic of the impression the paper produced on Mendel's contemporaries. Darwin did not refer to it in any of his writings, although he does refer frequently to other investigators in the same field who preceded Mendel or were of his day.

The study of hybridology, as it was called, had been extensively followed by the older hybridists, Kölreuter (1760–66), Knight (1779), Gaertner (1792–1850), and Naudin (1863), using the experimental approach. Much interesting information had accumulated about the character of hybrids and their fertility or sterility, as well as the infertility between species, but no fundamental principles of heredity had come to light. We can understand today why this early work in hybridization failed to detect the underlying principles. The experiments involved, as a rule, materials that were too complex to make a simple analysis possible. Yet one of these botanists had come very near to the conclusion enunciated by Mendel. The French botanist, Naudin, expressed in 1863 the idea that the elements derived from the parents separate in the hybrid. Some of the characters of the parental forms may then reappear in the next generation. But in the absence of sufficient numerical data and controlled tests this discovery falls far short of Mendel's work. Mendel succeeded where others had failed because he chose simple cases with clear-cut differences, and also because his analysis was based on sufficient quantitative data. From these he was able to formulate a few simple rules; these were checked by suitable tests and the postulates verified.

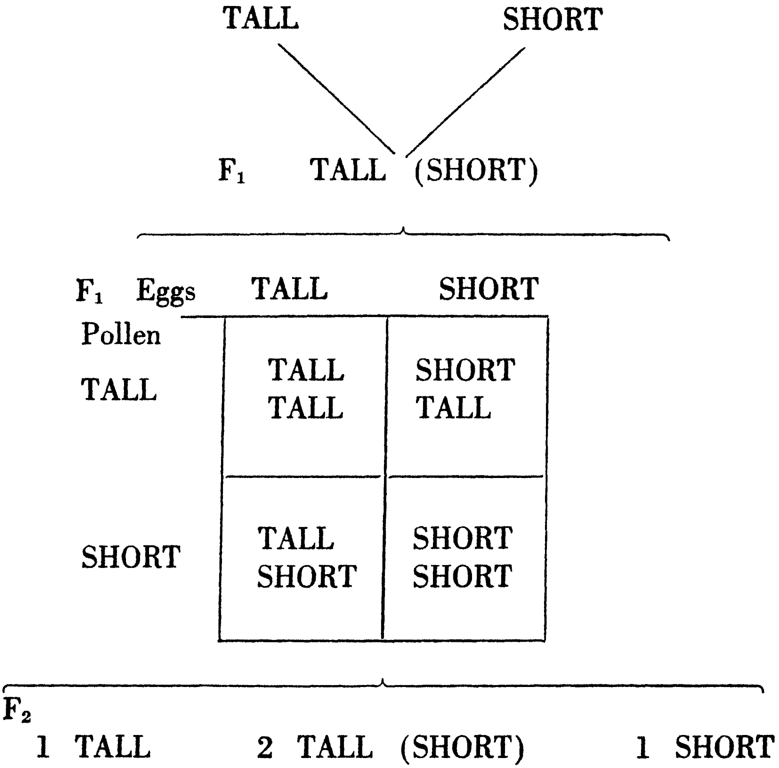
In any consideration of the bearing of Mendel's work on the theory of evolution, and more particularly on the mutation theory, there are two important ideas that should be carefully kept apart. One of these is concerned with discontinuous variation, and the other with the relation of variation to heredity. Mendel did not raise the question of the discontinuity of variation. It is true he made a careful selection of his materials of such a sort that the pairs of characters that entered the cross were sharply defined one from the other. Today we think of these characters not only as discontinuous in a descriptive sense, but as having arisen—in an historical sense—by an abrupt change from some antecedent character. Mendel was not really concerned with the origin of the characters he studied, but with their fate: in a word, with their behavior in heredity; and in order to study their behavior he followed the procedure of his predecessors. He brought the contrasted characters together in a cross.

The second consideration concerns what happens when two such characters are brought together. Here, also, there are two questions: the character of the resulting hybrid, and the kind of offspring the hybrid produces.

Mendel found that the hybrids of the first generation (F_1) resembled, in the particular character considered, one of the parents (Fig. 18). He called this character the dominant one. In the figure the tall pea dominates the short one. He found this relation to hold in the seven pairs of characters he studied. The offspring (F_2) of the hybrid were of two kinds, in a ratio of 3:1. There were three times as many of the dominants as of the other kind—the recessives. Mendel also inbred individuals of this second (F_2) generation, and found that some of them came true to the dominant character, while others, also showing the dominant character, produced both dominant and recessive offspring in the ratio 3:1. The recessives of this second generation (F_2) produced only recessive offspring.

From this evidence, and other evidence of the same kind, he explained the results on the theory that one of the original races carried an element for the dominant character, while the other carried the contrasted character, the recessive. These are brought together in the hybrid. If, now, when the germ-cells of the hybrid are formed, the two elements that went into it are separated, then chance fertilization of any egg by any pollen grain (Fig. 18) will give the numerical results shown by the offspring, namely, a three-to-one ratio.

The essential part of this theory is that the *elements* that go into a combination do not combine, or suffer change, but



F_1 Eggs Pollen	TALL	SHORT
TALL	TALL TALL	SHORT TALL
SHORT	TALL SHORT	SHORT SHORT

FIG. 18. *Diagram illustrating a cross between a tall and a short pea-plant. In the square are shown the recombinations resulting from the random meeting of the two kinds of pollen and the two kinds of egg-cells of* F_1 *giving the ratios of 1:2:1.*

reappear again when the germ-cells of the hybrid are matured; and they come out in equal numbers. This is Mendel's first law. It has been found to have the widest application, both to animals and to plants, both high and low in the scale.

There was much more in the discovery than discontinuity of characters in inheritance. It established the fact that the phenomena of heredity could be dealt with on a numerical basis, and that behind the characters there are units in the germinal materials that retain their individuality quite aside from the characters shown by the hybrid parent that carried them.

By implication, furthermore, there is in Mendel's discovery a fact that should have had a far-reaching influence on the method of studying heredity; namely, that characters shown by an individual are, in themselves, not a sufficient measure of the germinal constitution of the individual. For example: the hybrid may resemble one of the parents so closely that there is no measurable difference between it and the corresponding characters of the dominant race from which it came. The original race breeds true to that character, while the germ-cells of the hybrid are of two kinds. If the fundamental significance of this fact had been appreciated, the study of variation and heredity might have avoided the false move made by the early school of biometry, which based its theory on the assumption that the character of an individual may be taken as a measure of its origin and of its potentialities.

In the example given, the first-generation hybrid was like the dominant. As I said, all of the cases given by Mendel were of this kind. But today we are familiar with the fact that all first-generation hybrids are not of this kind. In many cases the hybrid shows an intermediate character. As an example, the cross between a red-flowered and a white-flowered four o'clock (Mirabilis) gives a pink-flowered hybrid (Fig. 19). Nevertheless Mendel's rule still holds, for when the germ-cells ripen in such a hybrid (Fig. 20) they are of only two kinds: red-producing and white-producing as shown by their progeny, which are in the ratio of one red to two pink to one white. The results of this tend to show that even the character of an intermediate hybrid is not an index of what its germ-

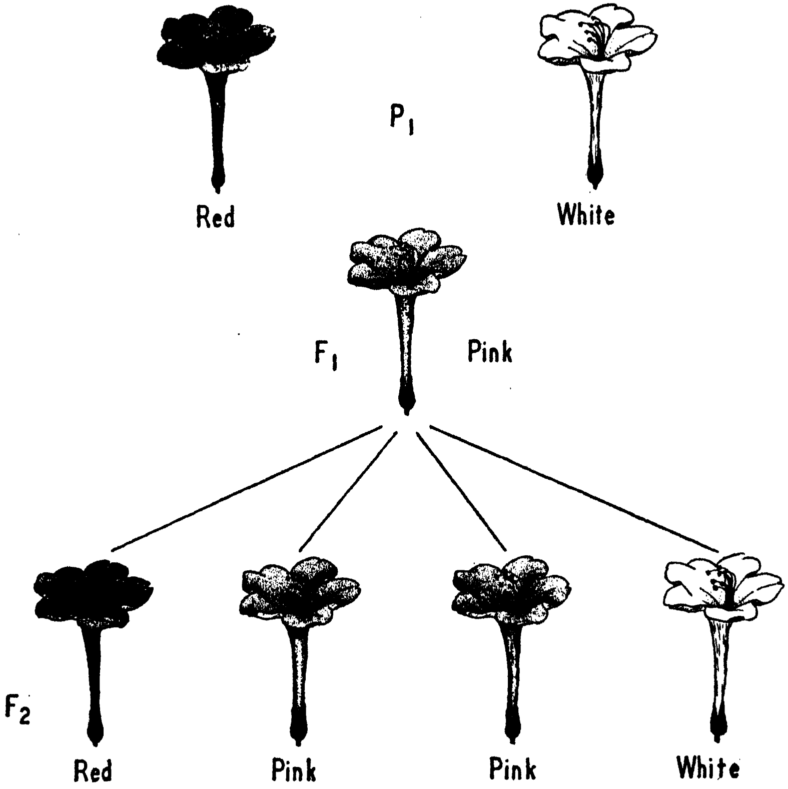


FIG. 19. *Cross between a red-flowered and a white-flowered plant of Mirabilis jalapa (4 o'clock). The hybrid (F_1) is colored pink, which after self-fertilization gives (in F_2) 1 red to 2 pinks to 1 white.*

cells are like, or a measure of the contribution of the two parents; for in appearance it may incline towards one or the other in different cases.

MENDEL'S SECOND LAW

Mendel's first law relates to the mode of transmission of a single pair of characters in a cross. His second law states what happens when two pairs of characters enter the cross at the same time. For example, yellow and green seeds of the garden pea are a single pair of contrasted characters and give, in the second generation, three yellows to one green. Round and wrinkled seeds form a similar pair and give in a cross three

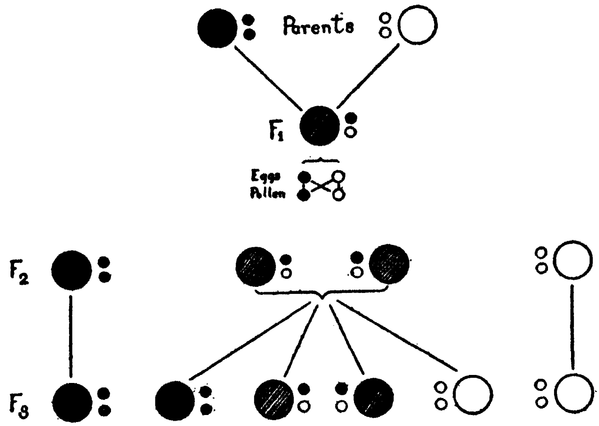
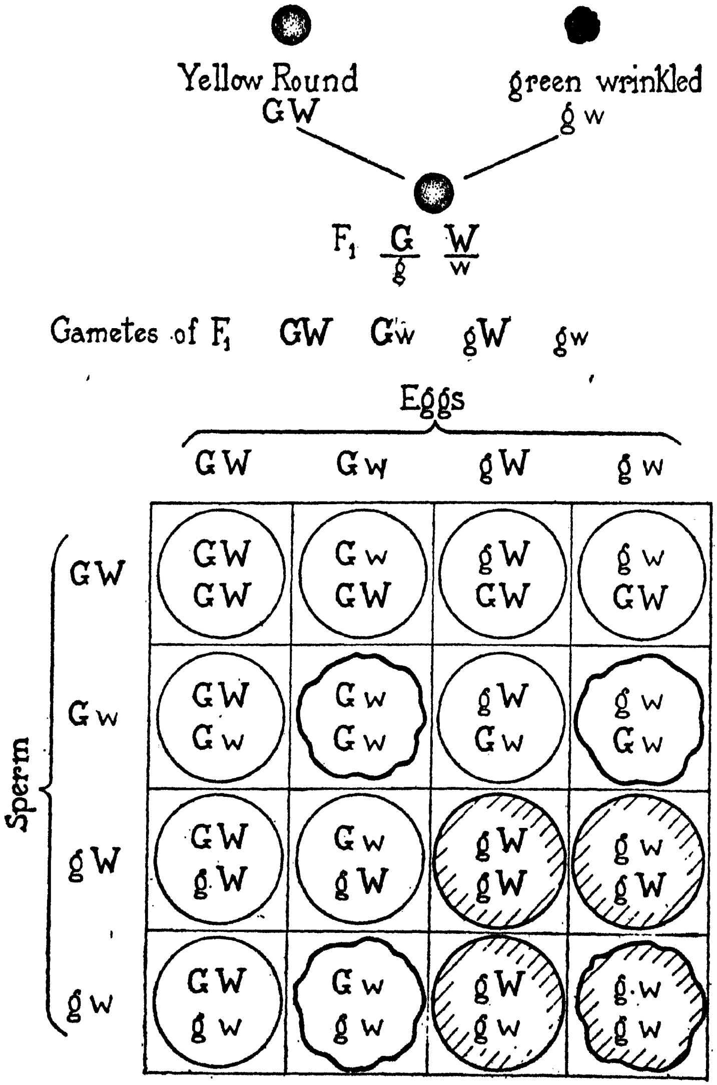


FIG. 20. *Diagram illustrating the behavior of the germ-cells (gametes) in the cross shown in Figure 19.*

rounds to one wrinkled in the second generation. When both pairs enter a cross at the same time, that is, when an individual that has yellow and round seeds is crossed to one with green and wrinkled seeds (Fig. 21), the hybrid has yellow and round seeds—the two dominant characters. When the hybrid is self-fertilized, four kinds of peas are produced, in the ratios of nine yellow round, three yellow wrinkled, three green round, one green wrinkled. This ratio, Mendel showed, is expected if the two pairs of characters that enter the cross behave independently of each other.

At the time when Mendel formulated his two laws there was not enough known about chromosomes to have made it possible to interpret his laws in terms of the kind of cell-divisions



	GW	Gw	gW	gw
GW	GW GW	Gw GW	gW GW	gw GW
Gw	GW Gw	Gw Gw	gW Gw	gw Gw
gW	GW gW	Gw gW	gW gW	gw gW
gw	GW gw	Gw gw	gW gw	gw gw

FIG. 21. *Cross between a pea with yellow round seeds and one with green wrinkled seeds. The offspring (F_1) have yellow round seeds. Four kinds of pollen grains and four kinds of egg-cells are produced, giving the 16 combinations shown in the square, which consists of 9 yellow round to 3 yellow wrinkled to 3 green round to 1 green wrinkled.*

that take place at the maturation of the germ-cells. Only during the last quarter of the last century were the changes that take place at this time gradually worked out and their possible relation to heredity discussed. It was largely due to the speculations of August Weismann that the significance of this relation became impressed on biologists, although he gave an entirely erroneous account of what takes place. After the re-discovery of Mendel's paper in 1900, the application of the chromosome behavior at the time of maturation of the germ-cell was first clearly pointed out by Sutton (1903), both for the first law (the segregation of the elements) and for the second law (the independent assortment of separate pairs of elements). Since that time a great deal of further evidence has been obtained which leaves no doubt that the chromosomes are the bearers of the hereditary elements, and that the changes that take place during maturation of the germ-cells supply the mechanism for Mendel's principles. This relation is illustrated in Figure 14, in which the pairs of chromosomes are represented as having come together just before the first maturation division. If the maternally-derived member of any one pair of chromosomes carries an element or gene for a given character, and the paternally-derived chromosome carries the allelomorph for the contrasted character, the two will be separated when the chromosomes separate and pass into different (sister) germ-cells.

When two pairs of factors enter the cross and one pair is carried in one pair of chromosomes and the other in another pair, and if (as is known to occur) these two pairs separate at random (i.e., independently of each other) when the cell divides, then the distribution of these chromosomes and their subsequent chance re-combinations at the time of fertilization fulfill the conditions of Mendel's second law.

Mendel also proved that, when three pairs of characters enter the cross, they are assorted independently in the germ-cells of the hybrid. If this relation were extended to apply to all pairs of characters the implication would be that each chromosome carries only a single hereditary factor, and since there are very large numbers of such characters, the number of chromosomes would have to be correspondingly large. But we know that their number is very limited. In fact, Mendel's second law has a much more restricted application than his first law. Our present knowledge of the continuity of the chromosomes would require such a restricted application of the second law—for if the genes are carried by the chromosomes, and the chromosomes remain intact, there could be, in any one cross, only as many independent pairs of characters as there are chromosome pairs. This question must next be considered.

LINKAGE

A great many cases have become known in which certain pairs of characters entering a cross together tend to remain together in later generations. This is known as linkage, and it has been shown definitely that linked genes are carried in the same chromosome. In consequence they do not follow Mendel's second law for two pairs of characters in the same cross.

Linkage, in turn, also has a restricted application, for occasionally, as we know, interchanges take place between members of the same pair of chromosomes. This interchange, which is called crossing over, involves whole chains of genes. Linkage and crossing over are correlative phenomena, and can be expressed by numerical laws that are as definite as those discovered by Mendel.

Both linkage and crossing over are therefore part of the system of heredity, and must be taken into account when dealing with the theory of evolution. Linkage insures that certain characters will more frequently be transmitted together, while crossing over means that characters, that first appear linked together, may be separated in the course of successive generations. The chances of such separation follow a definite numerical law, constant for specific pairs but different for different pairs of characters.

Linkage and crossing over may be represented by a simple example in which both characters and chromosomes are followed:

In Drosophila, black body-color and vestigial wings are both recessive characters whose genes are carried in the second chromosome. When one of these flies is crossed to a wild-type fly with "gray" color and long wings (Fig. 22) the offspring F_1 are like the wild-type. When a daughter (F_1) is backcrossed to a black vestigial male, 82% of the offspring are either black vestigial or wild-tpye (41% of each), and 18% are crossovers (9% of each); half have vestigial wings and gray color and half have long wings and black color (Fig. 22, lower line F_2). In the diagram, the gene for black, *b*, and that for vestigial, *v*, are represented in the same chromosome. The corresponding dominants (*B* and *V*) are not here symbolized in the corresponding chromosome (of the wild-type) but the chromosome is colored black. The F_1 female contains one of each of these chromosomes. She is crossed to a black vestigial male, in which both second chromosomes carry the two recessive genes, black and vestigial, because these recessive genes will not conceal in the offspring the characters brought in from the female, and will reveal, therefore, the kinds of chromo-

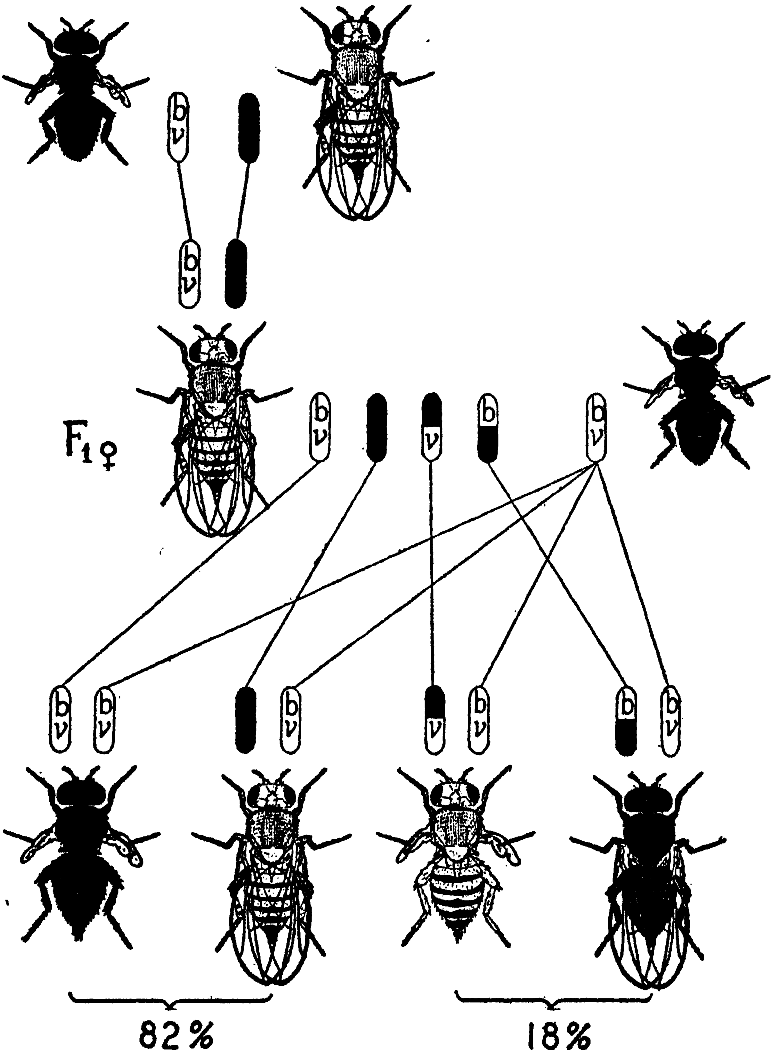


FIG. 22. *Cross between black vestigial and gray long wings (wild-type) Drosophila. The offspring* (F_1) *are gray long. A* F_1 *female is crossed to a black vestigial (double recessive) male. The genes for black and vestigial are linked, as are the corresponding dominants gray and long. In the* F_1 *female there is 18 percent of crossing over, as shown in the rods (chromosomes) in the middle of the diagram. The* F_2 *flies are of four kinds as drawn in the lower line.*

somes she carries. The results are shown in the lower line of the diagram. As stated above a large majority (82%) of the F_2 flies are like the two grandparents, viz., black vestigial and wild-type. This means that the two recessive genes that went in together have remained together, and the same statement holds for the corresponding dominants of the other chromosome. But in a minority of cases, 18%, there is an interchange of characters. It is evident that in some of the eggs of the F_1 females the second chromosomes have exchanged equivalent parts (see middle of diagram), and that the breakage has occurred somewhere between black and vestigial. In this case we measure the interchange by saying there is 18% of crossing over or recombination of characters.

In the next case (Fig. 23) a female fly with recessive white eyes and dominant gray color is crossed to a male with dominant red eyes and recessive yellow body-color. Here in each case a dominant gene and a recessive gene are together in the same chromosome, which is in this case the first chromosome or X-chromosome. The daughters (F_1) show the two dominant characters, red eyes and gray color. One of these is mated to a double recessive male with white eyes and yellow color, whose X-chromosome therefore carries only these recessives. It should be stated here that his other sex chromosome, Y, carries no dominant genes. The offspring are shown at the bottom of the diagram. The great majority (99%) of them are like the grandparents, and only 1% are crossovers. The latter are due to interchanges in the F_1 female between her two X-chromosomes.

In other cases, where other pairs of linked genes are involved, different percentages of recombinations occur. The percentages may be anywhere from less than 1% to 50%. But for any two particular pairs of characters the per-

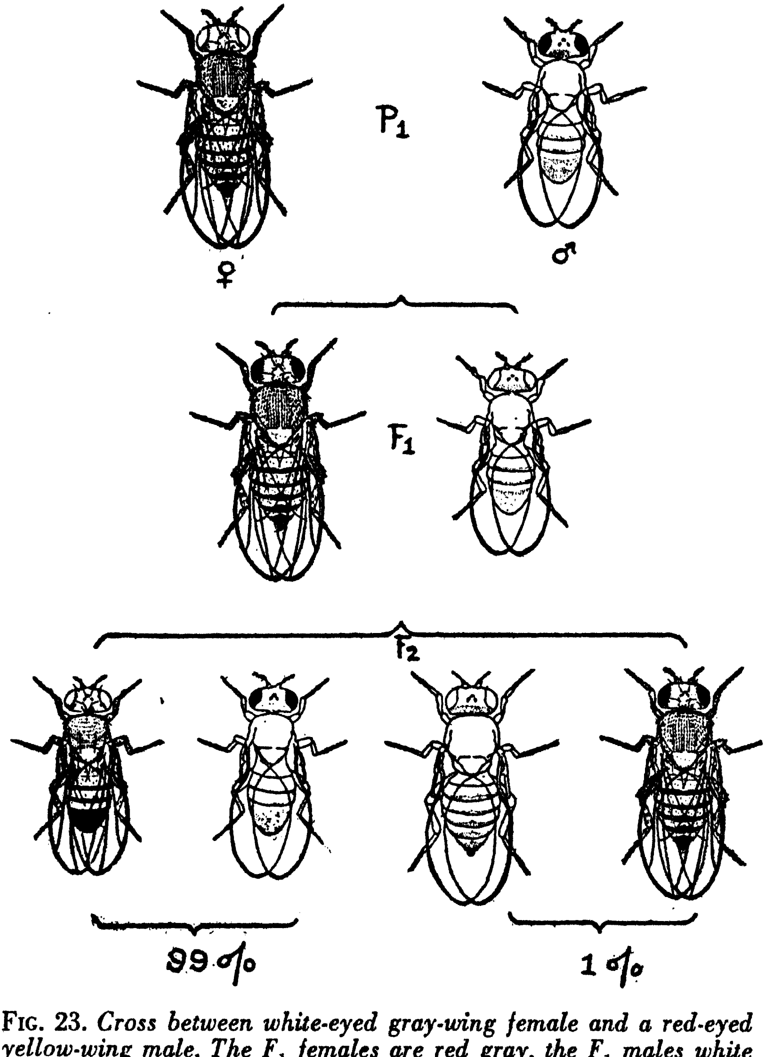


FIG. 23. *Cross between white-eyed gray-wing female and a red-eyed yellow-wing male. The F_1 females are red gray, the F_1 males white yellow. The F_2 offspring are of four kinds, as shown in the lower line. Crossing over occurs in the F_1 female to the extent of 1 percent. The genes are carried in the X-chromosomes, and the characters are said to be sex-linked.*

centage is constant. It is this constancy which makes it possible to build up chromosome maps representing the location of the genes in the chromosomes. For example: suppose the members of a given pair of chromosomes each carry two genes, *AB* and *ab* respectively, those in one chromosome being the partners (allelomorphs) of those in the other [Fig. 24 (1)]. If at the time of conjugation of these two chromosomes they should overlap at some point between *Aa* and *Bb*, as shown in Figure 24 (2), and if subsequently the parts lying to the right (viz. *aB*) should move to one pole of the dividing cell, and those lying to the left (viz. *Ab*) to the opposite pole, the results of this crossing over will be as shown in the diagram [Fig. 24 (3)]. This means that at the point where the threads have overlapped, the parts on each side of the union have re-combined to form a continuous thread.

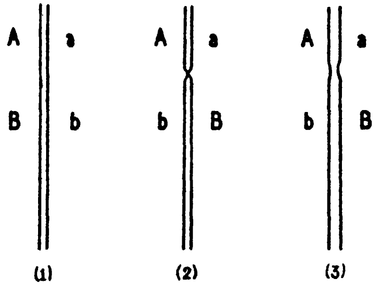


FIG. 24. *Diagram illustrating crossing over between homologous chromosomes, between the pairs of genes Aa and Bb.*

Now, if crossing over is as likely to take place at one level as at any other level along the length of the chromosome, then the nearer together the two pairs of genes happen to lie the less the chance of crossing between them: conversely, the farther apart they lie the greater the chance. On this assumption it is possible to localize the genes on the chromo-

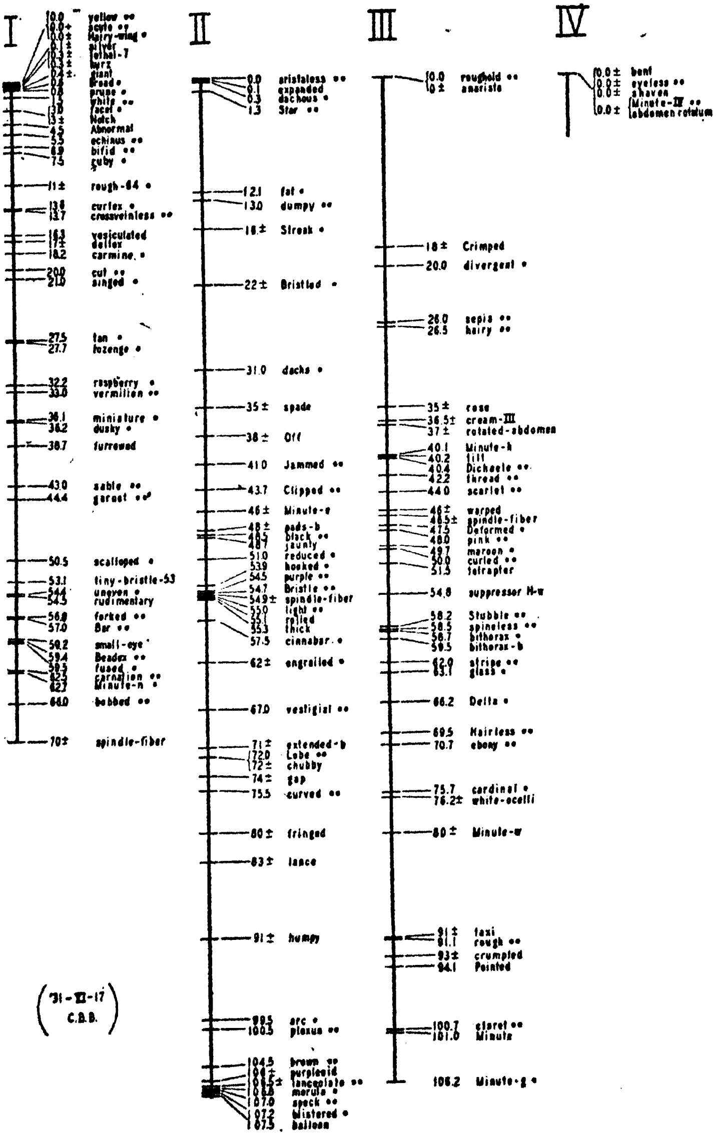


FIG. 25. *Chromosome map or chart of the location (loci) of the genes of the four chromosomes of Drosophila melanogaster. (A new map after Bridges.)*

some map. A chart of the four chromosomes of Drosophila, constructed on this principle, is drawn in Figure 25.

The usefulness of such maps for genetic work would alone justify their construction. This may be illustrated as follows. Suppose a new mutant character appears whose gene we wish to locate on the map. A cross is made with another stock carrying a gene of known position in the same chromosome.

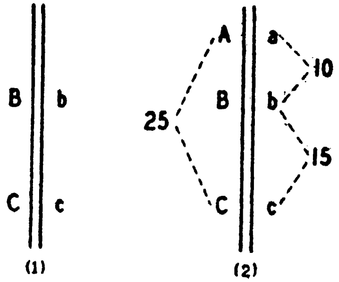


FIG. 26. *Diagram to show how a new gene, a, is located with reference to two genes, b and c, whose location in the chromosome is already known.*

The percentage of combination of the two characters is recorded. Suppose we call the unknown gene *c*; we compare it with one called *b* at a known level [Fig. 26 (1)]. We find it gives 15% of recombination, but the result does not tell us on which side of *b* the new gene lies. We then test *c* with another pair of genes, *Aa*, whose relation to *Bb* is known [Fig. 26 (2)].

If we find crossing over between *Aa* and *Cc* amounts to 25%, we infer that *Cc* must lie below *Bb*. But if *Cc* should give 5% of crossing over with *Aa* we infer that *Cc* lies above *Bb*. In this way the order of the genes in the linkage group is determined. By utilizing the numerical value obtained in this way, it is possible to predict very accurately how the new character will be inherited with respect to all other know genes in the species to which it belongs. In this sense the construction of such charts would be justified, but from the point of view of the constitution of the germinal material the charts have a more profound significance.

An important reservation must be made here—one that geneticists have always been aware of. We have assumed that the chance of crossing over is the same at every level of the chromosomes. As will be shown presently this may be inexact. The point is illustrated by a railroad time-table. The time a train takes between stations is a fair measure of their distance apart, but it is not exact. There may be grades or variations in speed, or waits at certain points in consequence of which the time between stations is not always an exact measure of their distance from each other. So it may be with the map distances. For, if crossing over should be more frequent in certain regions than in others, the map distances are only approximately true.

The interpretation of the map distance deduced from genetic data in relation to "distance" or length of the physical chromosome was discussed in 1913 by Sturtevant. Thus it was realized very early that the relation between the number of mutant genes that appeared in a chromosome might be expected to correspond to the size of the chromosome. When sufficient data had accumulated there was found to be a rough agreement of this kind. This evidence is much stronger today, with an increase in the number of known loci. Muller pointed out in 1914 that the few mutants recorded for the small chromosome IV favored this interpretation. The evidence derived from the apparent heaping up of mutants in certain regions, and the length of a section required for double crossing over in different regions was discussed by

Bridges (1919), and also by Bridges and Morgan (1923). Later, still stronger evidence bearing on this relation has come to light from several sources. The materials which formed the basis for this work were discovered from time to time in the regular course of study of genetic problems in Drosophila.

ABERRANT DISTRIBUTION OF PIECES OF CHROMOSOMES

It sometimes happens that a piece of chromosome becomes detached and is added to some other chromosome. This process is spoken of as *translocation.* Here the total number of genes is not changed, but their location and linkage to other genes is affected. In other cases of translocation, the broken piece may be present together with two normal chromosomes. This is called *duplication.* An individual carrying such a duplication has certain genes in triplicate, and usually dies, unless the piece is very small.

In a third case a section may be totally lost. This is called *deficiency.* Such individuals have only one set of certain genes. If the deficiency is too big the individual dies as a rule, but if small it may live. It is interesting to note that for a given section deficiency is more likely to be disastrous than duplication.

While cases of translocation, duplication, and deficiency had occasionally been met with and described by Bridges and others in pedigree material, their frequency has been very greatly increased by treatment with X-rays.

Now it has been known for a long time that radium and X-rays may produce effects on the chromosomes without permanently injuring the rest of the cell. Effects of the kind were described by embryologists before X-rays were used by geneticists. The chromosomes may be broken up or clumped, or affected in other ways. Irregularities in the distribution of the chromatin at cell-divisions then result, and in extreme cases the cells die or fail to function normally.

There are four pairs of chromosomes in Drosophila melanogaster (Fig. 27) called I, II, III, IV. The first (I) is the X-chromosome, two of which are present in the female, and one in the male, which also has a Y-chromosome, generally designated as one of the sex-chromosomes. The second pair (II) consists of bent chromosomes. The third pair (III) is also bent and slightly longer than the second. The fourth (IV) pair consists of minute chromosomes, round or slightly elongated.

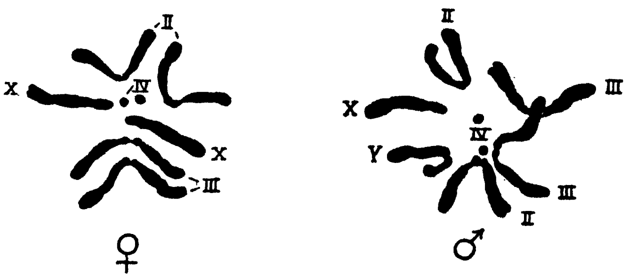


FIG. 27. *Somatic chromosome groups of female and male Drosophila melanogaster.* (*Original by Dobzhansky.*)

Each of the chromosomes contains a considerable number of known genes which serve as "markers." The genes in any one of these pairs tend to remain together, and are said to be linked in inheritance. Owing to the presence of markers (known genes) in these chromosomes, it is possible to follow in great detail the exceptional changes that may spontaneously take place on rare occasions or which are induced by X-ray treatment. The study of the relations that result from these disturbances of the chromosomes goes back seventeen years. Because of their bearing on the arrangement of the genes in the chromosomes it was at once realized that crucial evidence might be obtained from this source.

The history of losses from chromosomes (deficiencies) began with Bridges' discovery in 1914 of a deficiency involving the forked-bar loci (Bridges, 1917). Deficiencies for other loci (vermilion, facet) were shortly found by Bridges; and Mohr studied in detail the case of Notch-8 deficiency which involves a section of the X-chromosome in which several mutant genes are known. The first case of a large deficiency from the middle part of the X-chromosome was described by L. V. Morgan in 1925; the chromosome, from which many marked loci were lacking, was found cytologically to be much shorter than the normal chromosome.

The first case of translocation was reported by Bridges in 1919. In this case a section normally lying on the right end of the second chromosome was transposed onto the third chromosome. The length of the transposed section was, however, so short that chromosomes involved in the translocation appeared to be normal cytologically. Six years later the first case of a translocation leading to cytologically visible changes in the structure of the chromosome was reported by Stern. Stern described an attachment of a fragment of the Y-chromosome to the spindle-fibre end of the X-chromosome. These translocations, as well as some found later by Stern (1929) and by Sturtevant (Dobzhansky and Sturtevant, 1931), appeared spontaneously. It has more recently been shown by Muller (1928), Weinstein (1928), and many others, that the frequency of translocations is greatly increased by X-rays or radium treatment.

In spite of the variability of the mode of origin of translocation, some rules hold true for all of them. One of these rules is that "new" chromosomes having more than one spindle-fibre attachment, or chromosomes having no spindle-fibre attachment, do not persist, apparently because these conditions are incompatible with the continuity of the "new" chromosome. The other rule, which holds true in a large majority of the known translocations, is that crossing over is considerably reduced in some parts, or even in all parts, of the chromosomes involved in the translocation (Dobzhansky, 1931).

The history of the discovery of inverted pieces within a region of a chromosome is an old story, and involves in principle Sturtevant's work and that of Muller in 1913. It began with the discovery of what was known as a *crossover suppressor*. Many of these crossover suppressors turned out later to be due to inversion of sections of chromosomes (Sturtevant, 1926, 1931). It is interesting, as shown by Sturtevant (1921), and Sturtevant and Plunkett (1926), that two different species of Drosophila, namely, melanogaster and simulans, differ from each other by inversion of a section of the third chromosome.

Cytological studies of translocations have led to results which have a bearing on the problem of spatial relations of genes within the chromosomes.

In one of the experiments of Painter and Muller on the effects of X-rays, a large piece of the X-chromosome (Fig. 28) was destroyed (the unshaded part). The two ends which remained came together. This happened in one of the germ-cells of a male. When this affected sperm-cell fertilized an egg (of the attached-X stock) the cells of the daughter contained the chromosome group shown in Figure 28.

Comparing the size of the piece of the X-chromosome (composed of the two original ends) with the normal

X-chromosome, it is seen to be unexpectedly large (about half as large as an X), if judged from the amount that remains in the piece of the original X of the genetic map; i.e., if it consists only of the two black ends of the rod in Figure 28.

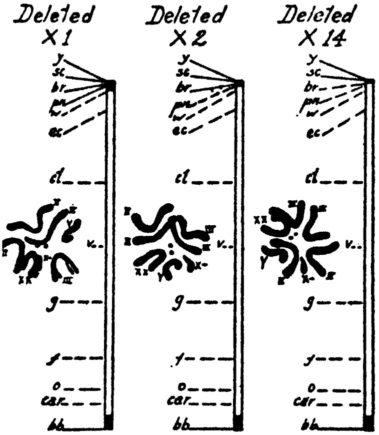


FIG. 28. *The three figures show the deletion of more than half of the middle of the X-chromosome. The two ends have rejoined. The relative size of the rejoined ends (X) is seen in the three drawings of the respective chromosome groups. (After Painter and Muller, Journal of Heredity.)*

For example, the entire length of the genetic map of the X-chromosome may be taken as seventy units on the chromosome map. Only a few of these units (about three) are represented in the united ends of the deleted chromosome, yet the piece, as seen in the cytological map, is more than half the length of one of the X-chromosomes (i.e., it is about thirty-five units long).

From this Muller concluded that the distances on the genetic map are not an exact representation of the distances between the genes. In other words, crossing over occurs at different rates in different regions of the chromosomes, just as the railroad train makes different speeds at different parts of its course—faster here, and slower there—while the linear order of the towns remains the same.

Dobzhansky reached similar conclusions at the same time (Figs. 29, 30), but in a somewhat different way, since his conclusions were based, not on what was left behind, but on the sizes of pieces that were translocated.

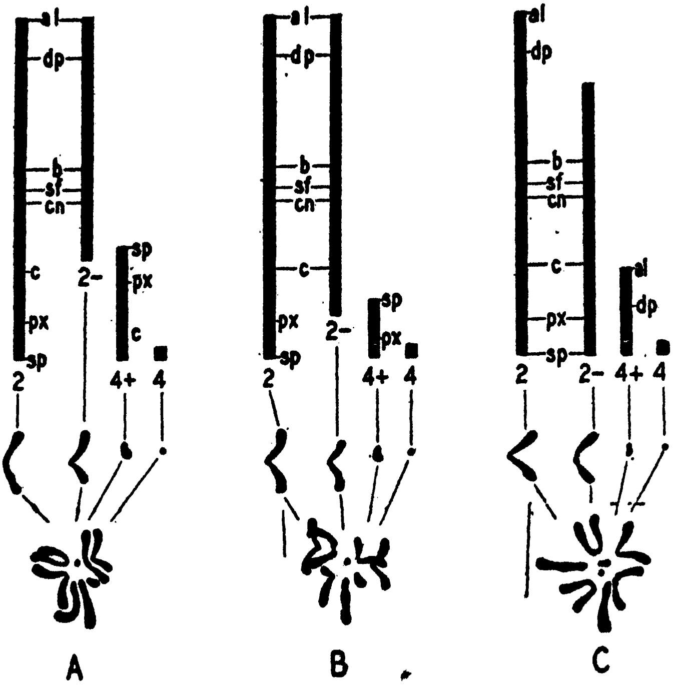


FIG. 29. *In A and B the "lower" part of chromosome II has been transferred to chromosome IV. The transferred piece in A is longer than that in B. In C the upper part of chromosome II has been transferred to chromosome IV. The relative sizes of the transferred parts of the genetic maps (above) and of the cytological figures (below) are represented. (Original by Dobzhansky.)*

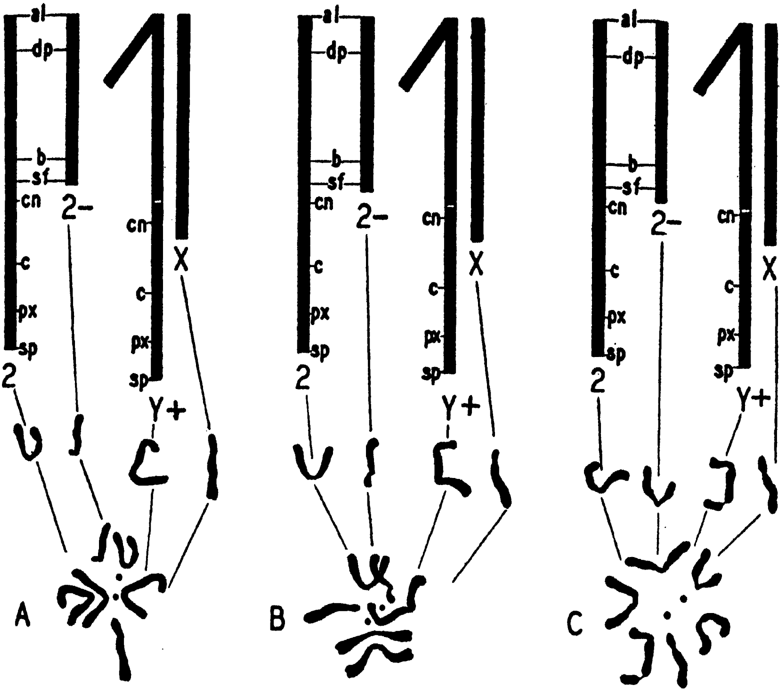


FIG. 30. *Parts of chromosome II (of slightly different lengths) have been transferred to the end of the Y-chromosome. (Original by Dobzhansky.)*

Figure 29 will serve to illustrate Dobzhansky's results. In *A*, *B* and *C*, a piece of the second chromosome of Drosophila has broken off and attached itself to one of the small fourth chromosomes. The piece is longer genetically in *A* than in *B*. The translocated pieces themselves are seen in the lower part of the figure as they appear in the actual chromosome groups. The sizes of the pieces in *A* and *B* are equal cytologically. This is interpreted to mean that the middle of this limb of the chromosome (the *c-px* interval) is much longer genetically than cytologically. The translocation of a piece from the opposite end of the second chromosome is shown in Figure 29c. Here the translocated section is relatively much larger genetically than cytologically.

In Figure 30, three translocations are represented, involving the transfer of a piece of the second onto the Y-chromosome. The piece translocated in *A* is, genetically, insignificantly longer than in *B*, and in *B* only insignificantly longer than in *C*. But as shown in the drawings of the chromosome groups the cytological sizes are strikingly different. This means that distances between genes lying in the middle of this chromosome are relatively greater cytologically than genetically.

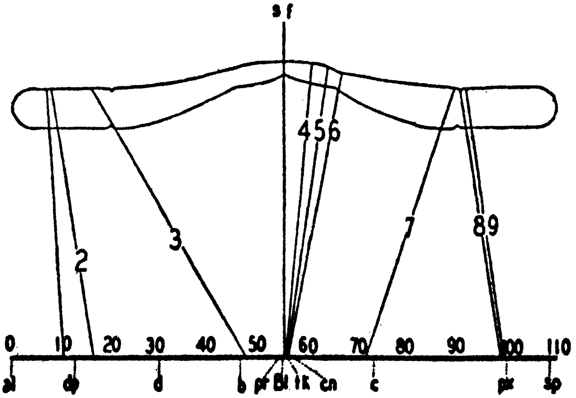


FIG. 31. *Above the actual (cytological) second chromosome is represented; below, the black line represents the genetic map drawn to the same scale. The vertical lines show the comparative lengths on the chromosome and on the genetic map.* (*After Dobzhansky.*)

The conclusions from evidence of this sort are summarized in Figure 31, where the second chromosome is represented above and the genetic map below, drawn to the same scale—the vertical lines indicating the relative lengths of estimated regions in the two chromosomes. It is evident that at the middle of each limb of this cytological chromosome the genes are nearer together than the genetic map indicates, and that this relation is reversed in the middle of this chromosome.

One of the most interesting types of translocation involves an exchange of halves of two different chromosomes. Two chromosomes break apart and the resulting four fragments reunite to form two new chromosomes. For example, if, in an individual (Fig. 32a above), two chromosomes of *different* pairs should interchange halves, the resulting individual would be like that of Figure 32a, below. In the latter all the original genes are present, but the four chromosomes are differently combined. Now, if the two *a*'s should cross, an individual with the composition of *b* might result. If in the maturation of the germ-cells of such an individual like parts come together, a cross-shaped figure, such as shown in *c*, would appear. When the chromosomes of the cross pass into the spindle of the dividing cell they will open out into a

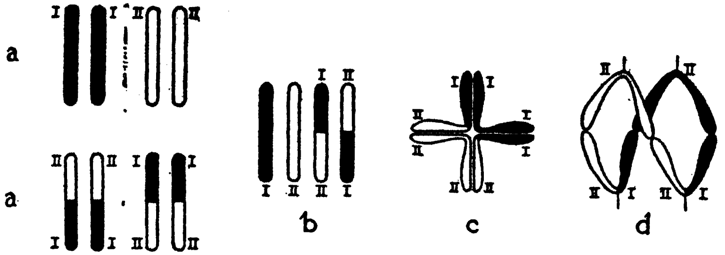


FIG. 32. *Diagram illustrating the resulting configuration of chromosomes (c and d) when there has been an exchange between different chromosomes as indicated in the figure by the black and white. In a and a an exchange between chromosomes I and II is shown. In b a chromosome group is drawn in which there are two interchanged chromosomes and two whole chromosomes. In c the coming together of these four chromosomes is shown, and in d the results of the opening out of this cross into a twisted ring.*

twisted ring, as shown in *d*. Two chromosomes now pass to one pole and two to the other, alternate chromosomes of the ring passing to opposite poles. As a result, each daughter-cell gets all the genes of chromosomes I and II. In this example, one cell gets the two intact chromosomes (derived from one parent) and the other cell gets the two chromosomes with exchanged halves (derived from the other parent). This is the actual situation in most of the species of Oenothera in which the presence of rings is a constant feature involving, in some

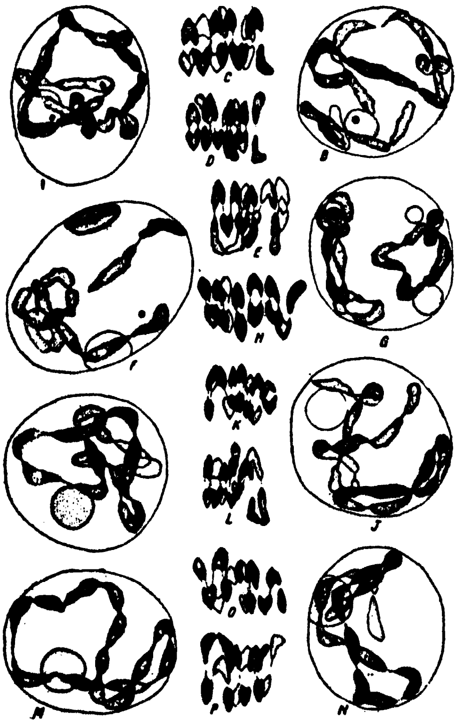


FIG. 33. *Eight nuclei of Oenothera just before the formation of the first maturation spindle (as seen in the figures in the middle where the chromosomes are moving towards the poles).* (*After Cleland and Oehlkers.*)

species, two pairs of chromosomes, in others, more pairs. This means that in so far as the genes are involved in rings, the maternally derived genes and the paternally derived genes go into different germ-cells. In other words: free assortment of chromosome pairs does not take place. This result is an exception to Mendel's second law.

In this connection many results in the genetic behavior of Oenothera have found an explanation in a suggestion that came originally from Belling, namely, that in certain cases there have been reciprocal translocations between halves of non-homologous chromosomes, as explained on page 87, (Fig. 32a, a[1]). The most characteristic feature of the genetics of this genus is the separation in the maturation stages of large complexes of chromosomes (Fig. 33), instead of single chromosomes.

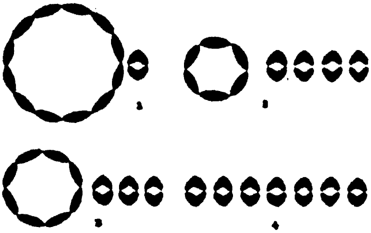


FIG. 34. *Diagram of rings in species and varieties of Oenothera. In 1, a ring of 12 and one pair (Oe. lamarckiana); in 2, a ring of 6 and 4 pairs (Oe. rubrinervis); in 3, a ring of 8 and 3 pairs (Oe. rubricalyx); in 4, there are 7 pairs (no rings) (Oe. blandina and deserens). (After Cleland.)*

The different species of Oenothera are characterized by the presence of different numbers of free chromosome pairs and of rings (Fig. 34). The mode of inheritance of the characters in these species has been shown to be intimately connected with the condition of the chromosomes at the time of reduction. The result has not only led to the clearing up of many obscure points of inheritance in Oenothera, but has even made it possible to predict what the configuration of the chromosome (the number of rings and pairs) will be, and also the behavior of certain genetic factors in the progeny of different species-crosses (Cleland, Sturtevant, S. Emerson, Blakeslee). Linkage here takes on a new relation if the term is extended to include whole chromosomes that move together to the same pole. In some cases, when a ring is formed of all the chromosomes the result is such that all the maternally derived chromosomes of the ring move to one pole and the paternally derived to the other. In addition, it is probable that prior to the formation of the rings there may also be crossing over between the individual parts of chromosomes comparable to crossing over in other forms that do not have rings.

CONCLUSIONS

The Drosophila maps that are now made, corrected according to the information from the experiments on translocations, show that there is no crowding of the genes, but a fairly even distribution except in the X-chromosome. This means that the genes themselves are distributed uniformly in linear order throughout the chromosomes. It is the unequal amount of crossing over in different regions that leads to an apparent crowding in certain regions.

It is this exact, detailed information that has completely transformed the old speculations concerning the principles of heredity into the laws of genetics. And because of this verifiable information the study of genetics has become one of the most advanced fields of biological work. Until the principles of heredity were placed on this footing, the theory of evolution rested on a very insecure basis.

CHAPTER IV

VARIABILITY AND ARTIFICIAL SELECTION

AT the time when Darwin wrote the *Origin of Species*, there was in the literature a good deal of scattered information concerning variation. This supplied Darwin with most of his materials. In addition, Darwin was familiar at first hand with a wide range of general observations on the variability of animals and plants under domestication. Between 1859 and 1900, a great deal more work of this kind was done in bringing new varieties under cultivation and in improving, by artificial selection and isolation, many of the forms already in cultivation. Valuable additions to our stocks were made, usually by animal and plant breeders. Much of this work, but not all, was haphazard and done by rule-of-thumb. The intention was generally to obtain more valuable commercial products. The procedure was not the best way of discovering the underlying principles that produced the desired results. For practical results it may have been a sufficient method, but it was laborious and wasteful to a high degree.

With a knowledge of the basic laws of heredity, it is now possible to obtain the same results with much less expenditure of time and money. In fact, in most experiment stations, the importance of carrying on breeding work more intelligently has received wide recognition. The information that is gained by clean-cut, controlled experiments on pedigree material is certain to replace in large part the trial-and-error methods that have been in vogue in the past. On a much greater scale than ever before, wild forms are being brought into the laboratory and experimental garden; their properties closely studied in pedigree cultures; their variability measured; their mutation rates recorded; and their combinations with other wild-types and with domesticated types examined. We are in the midst of this work at present. Whether one does or does not agree that evolution by means of artificial breeding and selection is essentially the same process as that which has taken place in nature, it will be conceded that what we learn by experimental methods concerning the kind of evolution resulting from artificial selection may come to have, as Darwin thought, a very significant bearing on our interpretation of evolution in nature; for, there is already enough information at hand to demonstrate convincingly that the laws of variation and of inheritance are the same in both.

ENVIRONMENTAL AND GENETIC VARIABILITY

If the individuals of a biological population are measured or weighed, the data can be arranged in the form of graphs (Fig. 35). One of the most common graphs corresponds to the curve of probability (Fig. 36). There are found to be more individuals of medium size and fewer in each class that are shorter or longer. Breeding experiments have shown that these differences may be due either to the influence of external conditions (the environment) or to different kinds of internal or genetic factors. For example: external influence affecting the growth-stages favorably or adversely may determine the

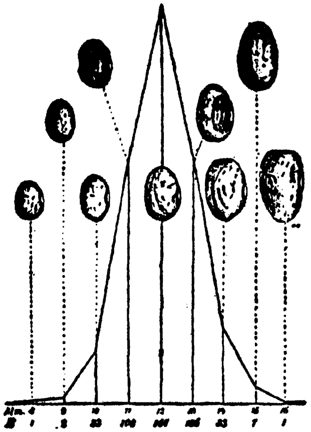


FIG. 35. *Diagram of beans of different sizes, the frequency of which is shown in the curve.* (*After de Vries.*)

size, or other property, of plant or animal. On the other hand, the size of an individual may be affected by hereditary factors, some making for larger, others for smaller measurements. Since these environmental and genetic factors may affect the individual, or any part of it, in practically the same way or in opposite ways, the problem of detecting which influence is producing the effect is not always a simple one.

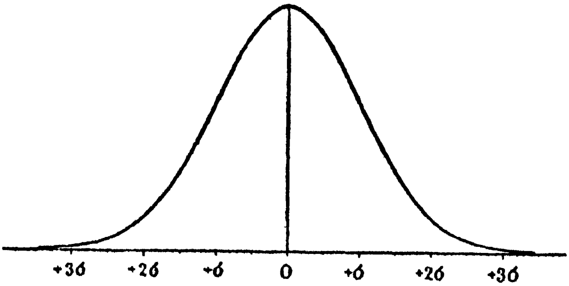


FIG. 36. *Typical frequency curve or curve of probability.* (*After Johannsen.*)

The outstanding work in this field was that carried out by Johannsen (1901), a Danish botanist. The clean-cut results of his experiments were due to a fortunate choice of materials; the fortunate circumstance was the pure or homogeneous character of the stock he used. This means that the internal or genetic factors were uniform in any particular individual (or technically, each individual was homozygous) hence any differences in the offspring produced by such an individual must be due to environmental influences. Johannsen weighed and measured the seeds of the Princess bean, and bred the offspring from each bean plant through successive generations. Individual homogeneity was present in these beans because they are self-fertile. Cross-fertilization between different plants rarely, if ever, takes place under ordinary conditions.

It can be shown very simply that any animal or plant reproducing by self-fertilization will, in time, become uniform for its genetic factors, no matter how complex in this respect it may have been at the beginning. An example will illustrate how this happens. Suppose we start with a heterozygous individual—that is, one in which the members of several pairs of hereditary elements or genes are different. Whenever two like genes meet to form a member of the next generation, that individual remains in later generations constant for this pair. If we consider only one pair of genes, there will be in the next generation three kinds in the ratio of 1:2:1; that is, two that are homogeneous to two that are heterogeneous for the two genes in question. But the heterogeneous will again split in the following generation into 1:2:1. In other words: the heterozygous individuals lose out in each generation, while the two pure lines steadily go on. Since all the descendants do not live, chance will sooner or later lead to the presence of two pure lines. In this way the Princess bean had been segregated into as many lines as there were original differences, so that when Johannsen began to study them he had pure lines or homogeneous material to work with. In all, Johannsen found nine pure races among the beans he started with. The descendants of each of the nine kinds he called a pure line.

Starting with the beans of any plant, Johannsen showed that it made no difference whether a small bean, a large one, or a medium-sized one is selected for the next generation (Fig. 37). Each such bean produces a plant whose seeds, collectively, are like the seeds of the parent. This is demonstrated by measuring a large number of beans from each plant. In other words, the data, if arranged in a graph, always give the same mean value for each pure line. The conclusion is obvious. Continued selection in a plus or minus direction, i.e., selection of large or small beans from homozygous plants of a pure line, will produce plants whose beans give exactly the same kind of population.

For the selection theory, whether artificial or natural, this discovery is of the first importance; for it shows positively that nothing can be accomplished by selecting variants due to environmental influences. This conclusion is in direct contradiction to the widespread belief that, since, by selection of different kinds of individuals in a *general* or mixed population the kinds of individuals produced in the next generation will be changed in the direction of the selection, this change will go on indefinitely. The apparent contradiction between this belief and Johannsen's conclusion is based, as will be shown, on the confusion between the variability due to the environment and that due to genetic differences.

Darwin's contemporaries seem to have understood that by selection of extreme individuals in any population, the next generation would be moved in the direction of selection. This

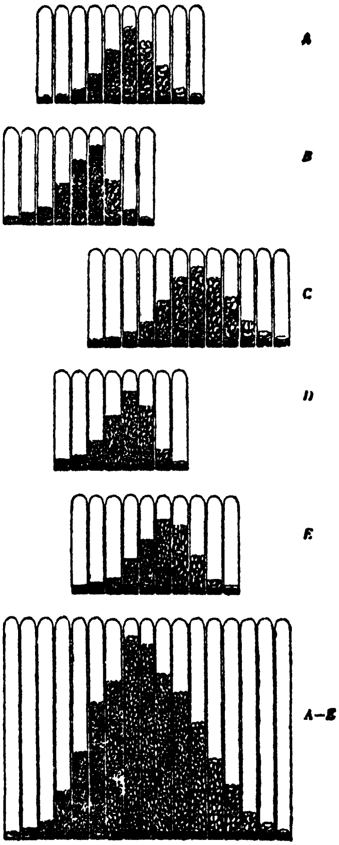


FIG. 37. *Diagram of beans arranged according to size. In A, B, C, D, E five pure lines are shown; in A–E a population made up of all these pure lines. (After Johannsen.)*

is true, however, only when different genetic factors are present, and even then the process soon comes to an end—as soon as these factors are sorted out. Nothing really new is accomplished, except that there are more of given kinds of individuals; but the limits of the original population are not transcended.

We understand today why this important discovery of Johannsen's had not been made before. All of the domesticated animals have separate sexes, and two individuals must combine to produce offspring. Many plants also are cross-fertilized. In a mixed population such a procedure will tend for a long time to keep up the racial mixture. Hence the problem cannot be put to a simple test, since the effects of environmental and genetic factors cannot always be distinguished by inspection when both are affecting the same character.

However, methods are known today by which it is possible to purify even the bi-parental races of their mixed genetic factors. One of the most practical methods, with this particular end in view, is to mate brother and sister in each successive generation, keeping always to the same line. In about ten generations the chances are that most, or even all, of the initial differences will have disappeared—that is, all the individuals will be pure for each pair of genes. They are then in condition for genetic experimentation; but in the earlier work on selection and even in some of the more recent work these preliminaries were seldom carried out.

An illustration will serve to show what may happen if an experiment is made with material that is not homogeneous; the experiment illustrates how an entirely erroneous conclusion was at first arrived at concerning the possibilities of artificial selection.

An extensive selection experiment on the color pattern of a race of hooded rats was carried out by Castle (1914). The first generation were offspring from commercial animals. Castle selected, in one series, those with the broadest dorsal stripe through successive generations and those with the narrowest dorsal stripe in another series, keeping the two lines apart. In the course of a few generations the two populations became measurably different. In one of them the dorsal stripe was on the average broader than that in the original group of rats, and in the other it was narrower. There was nothing in the results that was not consistent with the view that there had been a sorting out of genetic factors through selection, but Castle argued that he was dealing with the effects of a single gene, because when hooded rats are crossed to rats with a uniform coat color (all gray or all black) the offspring (F_1) are uniform, and when these are inbred they give, in F_2, three rats with uniform coat color to one that is striped. This Mendelian ratio proved, he argued, that a single genetic recessive factor was present. In fact, while this evidence does show that the striped coat is due to a recessive gene, it does not show that, when present, its width may not be due to other genes. This is the real question at issue. An experiment carried out later by Castle showed clearly that the width of the stripe is due to modifying genes.

The test was made in the following way. Each of the selected races was first back-crossed to wild-type rats, i.e., rats with uniform coats. The offspring from each parentage were inbred and a second generation of hooded rats was obtained. These F_2 rats were then bred (again) to wild-type rats and their offspring inbred. Another group of striped rats was obtained. It was found that after back-crossing for two or three generations, the later striped rats began to change back towards the original group of striped rats from which the experiment started. The selected race with narrowed stripe changed in the direction of a broader stripe, and correspondingly the selected race with broader stripe changed toward a narrower stripe. In other words, the two selected types were more like each other.

The outcome is in accord with the view that modifying factors are present in the wild-type rats that affect the width of the stripe when it is present, but produce no visible effect in rats with uniform coat. The conclusion is obvious: in the original experiment the width of the stripe had been changed by sorting out in the two lines the modifying factors, there present, that affect the width of the stripe.

It is interesting to compare Castle's results with Johannsen's. Castle's selection seemed to change the race. This was because the genetic material was impure. Johannsen's selection produced no change because his material was pure from the start.

With this new knowledge modern genetics is now in a position to accelerate the process of selection, and to avoid many of the pitfalls that breeders encountered when the method of transmission of variations was not understood and hit-or-miss methods were followed.

INBREEDING

Nowhere else is this knowledge so important as in the maintenance of fertility in inbred races or strains. It has long been held by breeders that close inbreeding frequently leads to loss of vigor and a lowered fertility; indeed, this has often been held an inevitable consequence of inbreeding itself. We now know that while infertility may occur, it is not inevitable, and we also know how to avoid such injurious results.

One of the most important aspects of this work has been the clearing up of a widespread prejudice amongst animal breeders against inbreeding. The work in this field has led to an intelligent understanding of what takes place when close inbreeding is followed.

It is true that in the past breeders have sometimes produced valuable results, by means of inbreeding, without loss of vigor, even after the closest inbreeding. It is equally true that in other cases disaster has followed. Today we can give an explanation of both results on the basis of clear-cut genetic principles.

The older experiments with mice and rats seemed to show that in a few generations of inbreeding there was a deterioration both in the number of young born and in infertile matings. Later work on rats and guinea-pigs, especially that of King and of Wright, has shown that when proper precautions are taken, inbreeding may take place without deterioration of the stock—in fact, even an improvement is possible. King inbred brother and sister rats for fifteen generations. After the first six generations there was a steady improvement both in size and vigor.* This was true both for the closely inbred rats and for the controls that were not inbred. The average size of the litters was also maintained after twenty-five generations in the inbred strain.

Similar results were obtained by Wright. Starting with closely inbred guinea-pigs, he crossed them for twenty more generations. In most of the lines there was a steady decline in vigor, and some lines died out; but some of the lines remained in the same condition as at the beginning. The point here is that distinct strains developed in the course of the inbreeding, each strain approximately constant within itself for vigor and fertility.

Castle inbred Drosophila for fifty-nine generations, breeding from the more productive pairs. In the end the full vigor of the strains was held. The key to the situation is found by breeding from those pairs that are the most fertile. By close selection there need be no deterioration, *provided* at the start there were good qualities as well as bad in the material.

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* The food was insufficient in the six earlier generations.

The key to these results was found in some experiments with Indian corn, especially those of East and Shull. They found that the progeny of self-fertilized plants was inferior in size, productiveness, and vigor as compared with cross-fertilized plants of the same stock. This decline was most marked at first, became less, and finally came to a standstill. The explanation offered was that Indian corn contains numerous recessive factors causing decreasing fertility and vigor, and that these are automatically sorted out by close inbreeding. In other words, a field of corn consists of hybrids for factors, low and high, involving fertility. Inbreeding leads to homozygous recessive strains that are less fertile than the mixed or hybrid strains. This explains why there was at first a rapid deterioration, which soon came to a standstill. Experiments proved that this was the correct interpretation, for when two such low strains are crossed, there is usually an immediate return to the vigor of the original stock.

A more extensive series of experiments was carried out by Jones, at the Connecticut Agricultural Experiment Station, which confirms and extends the earlier work. The results of fifteen generations of inbreeding corn are shown in Table I. At the beginning seventy-five bushels per acre were produced. The inbred lines dropped from thirty-four to twenty-four bushels per acre. At the beginning the average height was 117 inches; at the end one hundred inches or less. After the ninth generation there was no "consistent reduction in yield."

When these uniform races are crossed to each other there is an immediate return to the original corn. Moreover, there is a remarkable uniformity of type in the hybrids. But if these are now self-fertilized there is again a falling off in size, productiveness and uniformity—repeating the story all over again.

In a general way the results of inbreeding are shown graphically in Figure 38, which shows that the outcome is much the same regardless of the number of heterozygous genetic factors present at the beginning (on the assumption that no linked factors are present).

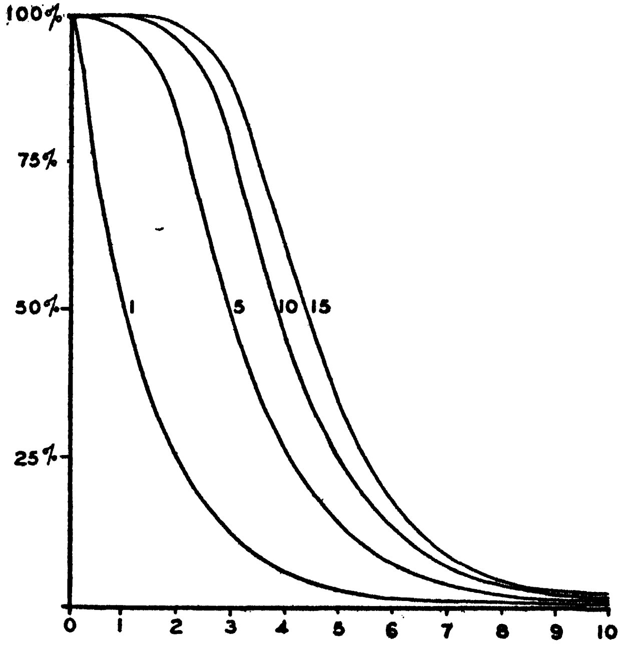

Fig. 38. *Diagram showing the percent of heterozygous individuals in each selfed generation when the numbers of allelomorphs concerned are 1, 5, 10, 15. (After Jones.)*

This account has ignored the question as to why dominant strains did not also appear after inbreeding that would be as good or perhaps even better than the heterozygous individuals. The most plausible answer is that vigor in corn is greater when both dominant and recessive genes are present, which is shown to be the case when two inbred recessive strains are crossed. Each then brings into the cross one recessive from one strain and one dominant from the other.

TABLE I

THE EFFECT OF SELF-FERTILIZATION UPON THE YIELD AND HEIGHT OF CORN

Four Inbred Strains from Leaming Dent Corn

NUMBER OF GENERATIONS SELFED	1–6–1–3, *etc.*		1–7–1–1, *etc.*		1–7–1–2, *etc.*		1–9–1–2, *etc.*	
	YIELD, BUSHEL PER ACRE	HEIGHT INCHES	YIELD, BUSHEL PER ACRE	HEIGHT INCHES	YIELD, BUSHEL PER ACRE	HEIGHT INCHES	YIELD, BUSHEL PER ACRE	HEIGHT INCHES
0	75	117	75	117	75	117	75	117
1	59	...	61	...	61	...	42	...
2	95	...	59	...	59	...	52	...
3	58	...	46	...	60	...	35	...
4	80	...	63	...	68	...	48	...
5	28	87	25	81	41	91	26	77
6	..	...	..	...	..	...	40	...
7	42	...	39	...	..	...	45	85
8	79	96	47	84	59	88	22	...
9	26	...	25	...	..	...	31	79
10	33	98	33	85	19	87	32	82
11	46	104	42	79	38	84	35	80
12	50	100	27	80	20	85	25	77
13	26	85	29	84	25	81	27	86
14	35	94	38	87	36	88	24	87
15	34	100	33	90	30	98	..	...
0	75	117	75	117	75	117	75	117
1– 5	64	87	51	81	58	91	41	77
6–10	45	97	38	85	39	88	34	82
11–15	38	97	34	84	30	87	28	82

HYBRID VIGOR

The converse case is what is known as *hybrid vigor*. It has long been known that by crossing different unrelated strains, or even varieties and sometimes species, the offspring may be more vigorous than either parent—even though they may be sterile, as is the case of the mule. As early as 1776 Kölreuter called attention to this, and the phenomenon is well recognized by breeders.

The most satisfactory explanation (one based on experimental evidence) appeals to the familiar fact that many *recessive mutants* are less viable, or less vigorous, or less prolific than the original type in which dominant mutant genes are present. Wherever these recessive genes have accumulated in a race, the double recessive or homozygous types are apt to be less vigorous. These recessive factors are known to be of many kinds. Now, if two stocks contain *different* recessives, each will probably also contain some of the wild-type *dominant* genes of the other stock. When brought together by crossing, the hybrid will get a dominant from each strain and these will counteract the recessives. Hence the return to greater vigor in such hybrids.

When the hybrid is selfed, on the other hand, there will be amongst the offspring some like the homozygous grandparents, some like the hybrids and other mixtures. Hence a wide array of types will appear whose *average* vigor or growth will be less than that of the first generation hybrids. If inbreeding continues different lines will be segregated out. This is exactly the picture we get when such a breeding test is made.

There are some reservations in this explanation, the most important being due to linkage of factors that do not completely assort in later generations. But when linkages are present they will in general act as though the group (chromosome) were a single factor, except when crossing over takes place. Even then, by suitable tests the resulting types can be sorted out by genetic methods.

INFERTILITY

Closely connected with these results on outbreeding and inbreeding and fertility is the question of the infertility that is often found when species are crossed, and the absence of infertility when a new mutant is bred back to its parent stock.

It has been argued that this is the most serious difficulty that the mutation theory has encountered, for if no incipient fertility is found when a mutant is backcrossed to its parent stock, how can we suppose that the infertility of wild species with one another has come about?

The infertility between species has sometimes been regarded as one of the criteria of species, although it is seldom utilized as such by systematists themselves. However, infertility between "species" is by no means universal. All gradations exist. So much so, in fact, that the statement usually runs: "when two species are fertile when crossed, but produce sterile offspring, the former may be regarded as 'true' species."

Let it be admitted that, while we cannot give a completely satisfactory answer to this question, the situation has so changed in recent years that geneticists no longer feel there is here any very serious difficulty, but rather a scholastic distinction that arose when species were regarded as specially created.

A few examples will serve to illustrate the nature of the infertility between species.

The passage of the pollen through the tissues of the ovary appears to be, on good evidence, a physiological process involving reciprocal relations between the two. Foreign pollen that does not come up to the requirements may fail to reach the egg-cells. All degrees of success are found in different crosses. When the pollen reaches the egg-cell and enters it, a series of complex events again takes place; failure in any one leads to the death of the potential embryo. This relation holds also for animal cells when the sperm reaches the surface of the egg. Infertility does not then appear to be an event that has been prepared for or evolved to prevent crossing, but a natural consequence of differences of various kinds between the different types.

In contrast to this situation a new mutant type differs from the parent type in one factorial difference, and unless this one happens directly or indirectly to affect the fertilization process or the early developmental stages, the two should be expected to be inter-fertile and produce not-sterile offspring.

But suppose a mutant type should establish itself and be separated from its parent type for a sufficient time to accumulate more and more differences. If some of these differences happen to affect the fertilization process, infertility may be expected. This argument meets, tentatively at least, the cross-infertility difficulty.

STERILITY OF HYBRID

In certain cases when species are cross-fertile, the hybrid is sterile; and the sterility of the hybrid has often been used as a criterion of good species when the infertility definition breaks down. Here modern genetics has something more definite to say.

The sterility of the hybrid is often due to a failure in a different part of the mechanism from that involved in infertility. At the time of ripening of the germ-cells, the paternally derived and the maternally derived chromosomes come together in pairs throughout their length. Subsequently they separate, move to opposite poles and pass into the daughter-cells that give rise to the mature egg-cell or sperm-cell. In those hybrids that are sterile, it has been shown that at this time there are serious disturbances of the mechanism. It has been found, for example, that the chromosomes may fail completely, or in part, to mate in pairs. As a result they become unequally distributed in the daughter-cells at the maturation divisions. This is especially true of some polyploid varieties. Now, it is known that cells lacking a complete set of chromosomes—having more or fewer of them—generally fail to produce normal germ-cells. As a result, the germ-cells are imperfect and the individual that carries them is sterile. All degrees of sterility exist in hybrids, and there has been found a close relation between sterility and the failure of the maturation stages, or even irregularities in the earlier germ-track itself.* On the other hand, the mutant differs from the parent type in only one genic change, and we know that one such change is not, as a rule, enough to interfere with the orderly union of the homologous pairs of chromosomes.

There are probably conditions other than those given, that are also conducive to infertility and sterility, and there is other evidence besides, showing that the sterility of hybrids is directly connected with mutant differences in the parental species.

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* The text refers especially to those cases where the hybrid reaches the adult stage and is vigorous; but in a great majority of cases the hybrid dies at an earlier stage, especially when the organ systems begin to differentiate. All gradations exist between such lethal effects on the body-cells and those referred to in the text where the effects appear in the germ-track.

In the light of these recent advances in our knowledge of fertilization phenomena, and of the maturation process in the egg and sperm, we need not, I think, be greatly disturbed by a contention whose importance has been exaggerated. We can formulate a possible, and even I think a probable, explanation of the cause of the infertility of many species and of the sterility of the hybrid in others. Granting that we need more information, nevertheless I think it more reasonable to accept what has been found as offering an approach to a solution, rather than exaggerate the difficulty standing in the way of the origin of species. For, after all, unless we are expecting to find extraneous causes or mystical somethings to explain the origin of species, is it not better to see whether their origin cannot be looked upon as a natural development, rather than to minimize what has been so laboriously gained because it does not agree with what may be only an artificial and scholastic attempt to raise a difficulty that may be less important than it has been made to appear.

CHAPTER V

ADAPTATION AND NATURAL SELECTION

DARWIN'S Theory of Natural Selection has been under discussion for seventy-two years. It has been accepted, on somewhat vague terms, by most zoölogists and botanists, and rejected by a few others. Darwin himself claimed only that it accounts for one of the ways in which evolution has come about. The mutation theory may seem to be today its only vigorous competitor, yet de Vries, the author of the mutation theory, stated that it was not in opposition to natural selection, but, on the contrary, helped to put natural selection on a firmer foundation. Some of those who have accepted the mutation theory have tacitly retained their adherence to the theory of natural selection as a general principle; others have shown reluctance to commit themselves to the general theory of natural selection. A few mutationists have rejected natural selection—at least, what they understand to be the essential doctrine of natural selection.

Of course no mutationist would deny that a new type must be able to survive and perpetuate itself if it is to take part in evolution; but this might be said to be only a commonplace. A mutationist might well insist that the essential part of Darwin's theory of natural selection is not survival, but Darwin's postulate that the individual variations, everywhere present, furnish the raw materials for evolution. This the mutationist would deny.

In what sense, then, have the catchwords "competition" and "the survival of the fittest" come to be generally regarded as the essential features of natural selection? Do these terms mean, for instance, that natural selection is an active agent in evolution, which in itself brings about progressive changes; or do they mean only that it acts as a sieve for the materials that present themselves as variations? If we think of evolution as an active process, is natural selection an agency capable of bringing about progressive changes, or does it not rather direct attention away from the real phenomenon, and offer at most only an explanation of the presence of certain types and the absence of others at any one period of geological history? The origin of these types—the real creative steps—not the preservation of certain of them after they have appeared, might rather be regarded as the essential phenomenon of evolution. If so, "the struggle for existence" and "the survival of the fittest" may express only a sort of truism or metaphor, and have nothing to do with the origination of new types out of antecedent ones.

These contrasts may be brought out more clearly by a statement of the converse situations. Suppose evolution had come about as a series of direct adaptive responses to the environment. In such a case natural selection would become practically meaningless, although the statement that this would lead to the survival of the fittest would still hold. In fact, Darwin did appeal to such responses in Lamarck's principle. He made this appeal whenever it gave, or seemed to give, a more plausible explanation than that based on chance variations, and he came in his later writings to depend more frequently on such an appeal. This seemed to put natural selection in the background, since Lamarckism would appear to be a more effective agency than natural selection in bringing about adaptation.

Since Darwin's time two interpretations of natural selection have been expressed: It has been claimed that "Darwinism" or "natural selection" means literally what Darwin said, or at least what his followers interpreted it to mean. Most of his immediate followers believed "Darwinism" to mean that selection of the innumerable differences always present will lead to progressive steps of evolution. Others might now maintain that, in so far as Darwin appealed to minute differences that are inherited, the principle of natural selection holds, even though these small differences are not everywhere present at all times but appear relatively infrequently as mutations. When present as mutants they would fulfill the requirements of Darwin's theory, namely, random variation and inheritance.

ADAPTATION

It has often been pointed out that the theory of natural selection has fallen into disrepute because of the reckless way in which naturalists have been ready to assume that any imaginary or fictitious use that could be assigned to a structure or function sufficed, *ipso facto,* to account for its evolution by natural selection.

Zoölogists and botanists have a pretty clear idea of what they mean by "adaptation." To deny that adaptation is a *scientific problem* at all, as has been done in fact, they consider a piece of stupidity due to the ignorance of those who make the assertion.

Whether this affirmation is stupid or not we need not try to decide, but it is possible to understand how it might be made; for if variation is a random process, the *origin* of a particular variation has no relation to its survival value, hence origin and survival have no causal relation, and if this is so, then only confused thinking could make one problem out of what are really two separate problems. In other words, if the survival of a new type depends on other relations than its origin, survival is an historical problem depending on environmental relations. Before deciding these questions, it may be well to examine how the principle of natural selection to explain adaptation has been used by students in different fields of biological work.

There is a suspicion that morphologists, who have been the most ardent students of adaptation, have often appealed to imaginary rather than known agencies in accounting for the evolution of adaptations. For example, the geological record tells us that the horse started as a small five-toed animal little larger than a dog. As time went on, it changed by degrees into a larger animal with fewer and fewer toes, until today the horse is left standing on one toe on each foot. So far so good: but the transformation is sometimes described as due to an adaptation to harder ground through survival of individuals with fewer toes. The single-toed condition is *assumed* to be an improvement, enabling the horse to run faster on open ground. Now, as a statement of an historical series of events, this descriptive evolution of the horse may be approximately correct, but the implication that the changes occurred because they were better adapted to hard ground is purely imaginary. As fiction the account may be allowed to stand, but if this fiction is to take the place of a scientific explanation of the origin of the horse, then exception might well be taken to it.

Adaptation would seem to be essentially a physiological process; but physiologists have been significantly silent about the origin of adaptations. They take for granted that adaptation exists to an extraordinary degree of refinement. In fact, physiologists may be said to have abundantly shown that internal adaptive adjustments exist and their problem is to exploit them. Whether their silence as to the origin of adaptation is due to contempt for the kind of speculation indulged in by the morphologists and evolutionists, or whether they are simply not interested in the problems of origins, I will not pretend to say; but I venture to think they are more than dubious about the scientific handling of this topic by morphologists. Somehow the procedure seems to physiologists different from work in their own field. Yet when, as has sometimes happened, they venture to discuss problems relating to evolution, they have been as venturesome as the most hardened morphologist, and have not infrequently resorted to mysticism or to metaphysics, which morphologists have, as a rule, tried to avoid.

Philosophers who have speculated about the origin of adaptations have not hesitated to invoke principles that transcend the realm to which scientists have restricted their labors. Bergson, for instance, starts with the postulate that to respond adaptively is the very essence of living matter. If his view is accepted, adaptation is not a scientific problem as generally understood, but an inherent property of living matter. His postulate will be discussed in a later chapter. All that need be said here is that few, if any, biologists are willing to accept so easy a solution of their problem.

In recent years an occasional physicist or chemist has entered the speculative field of evolution. Here at least we might expect carefully guarded statements, such as they would follow in their own fields where they are conversant with a tradition of high standards based on technical and experimental procedure. Yet the reverse is sometimes the case. What is even more surprising is that they should disregard the large amount of critical work that biologists have accumulated. The occasional chemist or physicist that I have in mind, acts as though evolution belonged to theology or metaphysics rather than to science.

I will not pretend to say how modern theologians in general look upon adaptation of living things. If, however, they regard living things as having been created in a single fiat by some extraneous kindly providence, it behooves them to study and account for some of the extraordinary manifestations for "evil" that have been set going. If a less crude approach is made, as in the case of Paley's watch, the argument is, in a sense, inverted, and the wonders of nature, which are assumed without critical consideration, seem to acclaim the presence of a beneficent creator. Whether this inference suffices without introducing an adverse agent to account for the tragedies and wastefulness of nature will bear examination, unless we choose to ignore everything in nature except that which seems wonderful and good. There is a wide difference of opinion as to whether questions of ethics fall entirely outside the proper field of science. It is certainly true that science does not pretend at present to handle ethical problems as it deals with other problems; but is it not rather daring to affirm that they belong to a realm beyond the reach of scientific study? When even a mathematician, Eddington, advises us to cherish whatsoever of our juvenile longings still persists, we can only raise the question whether we cannot today find a more satisfactory substitute for ethics than one based on a sentimental liking for finalistic principles which may be no more than conditioned reflexes established in childhood.

It is impossible to pass in review the immense number of structural adaptations known to zoölogists, but it is possible to give a few examples of several kinds. A fact of some interest becomes apparent at once, namely, that what are usually cited as adaptations are instances in which a species shows some unusual type of structure, i.e., one in which it departs from most of the other species of the group. In other words: it is the exceptional that is often referred to as a typical case of adaptation. The reason for this is apparent. The exceptions stand out conspicuously as specialties for some particular situation. Nevertheless, a moment's thought should show that the general problem of adaptation is not to be found so much in these particular occasional departures as in the totality of the relations of the organism to its environment which makes the perpetuation of the individual and of the species possible. The extreme cases catch our attention, and their special relation is sometimes more easily seen, or guessed at, than the more subtle physiological process that make all life possible.

A few of these special cases, commonly cited by zoölogists when discussing adaptations, will serve to illustrate the points just made. The resemblance of certain animals to their surroundings is supposed to protect them from their enemies. This is called protective coloration, and certainly some extraordinary examples of it have been recorded.

The resemblance of certain species, especially butterflies, to other protected species goes under the name of mimicry. It is described as a protection to the mimicking species.

Conversely there are animals that are conspicuously colored, and if they have also a nauseous taste or odor they are said to show warning coloration, on the assumption that their enemies may learn more quickly to let them alone.

The *individual* changes in color that such animals as flounders and other fish exhibit, imitating to some extent the color of their surroundings, are often cited as adaptations concealing the fish from their enemies.

These examples concern the organism as a whole in relation to its surroundings, more particularly their protection against the attacks of other animals, their real or imagined enemies. But as stated above, these are only special cases. The more fundamental relation of organisms to their surroundings is sometimes forgotten, or taken for granted by zoölogists, although these are really the significant features of living things that make their existence possible.

Of equal importance are the internal relations of the different organs and parts of each animal to other organs and parts. These relations constitute the central theme of classical physiology, and as such are generally regarded as problems for physiologists rather than as problems of adaptation. The digestion of food, the changes in the rhythm of respiration at rest and during activity, the maintenance of the chemical constitution of the blood, the excretion of waste products, the action of the secretion of the glands of internal secretion on other organs, functional hypertrophy, regeneration, and the healing of wounds are further fundamental attributes of life. The formation of antitoxins protecting the animal against diseases, furnishes many examples of regulative processes.

The reactions to stimuli received through the sense-organs, including the instinctive behavior of animals toward each other and to the inorganic world, are, par excellence, examples of adaptive behavior. The mating habits and the instincts connected with them, the care of the eggs and young are also adaptations that insure the continuity of the race. Associative memory and intelligence play an important rôle in the survival of the higher animals.

Finally, the exploitation of one species by another, as in the case of parasitism, must be regarded as a case of adaptation. In fact, some of the most striking cases of adaptation are found here. The cuckoo lays its eggs in the nests of other birds; flies and lice inhabit the bodies of other animals; many parasitic wasps lay their eggs in the larvae of other insects and even in the eggs of other insects; round worms and tapeworms live within the digestive tract of other animals. In all of these and many other ways, survival of the individual is made possible.

THE OBVERSE PICTURE

Even this brief rehearsal of some of the outstanding examples of adaptation in the animal and plant kingdoms may suffice to impress one with the *wonderland of science.* Since Darwin, the manifold adaptations of animals and plants have fired the imagination of biologists. We must be on our guard, however, lest continuous attention to the marvels of nature direct our thoughts away from the other side of the picture—the wastefulness, the cruelty, the tragedies of nature, as they appear to us. If it be said that this is true only when looked at from the standpoint of our human morality, economics, or psychology, the answer is that the assumed *beneficence* of nature, on which we like to dwell, is no less an interpretation from the standpoint of human society. Let us look then, if only for a moment, at the darker side of nature, as an antidote to too much sentimentality aroused by a study of her perfections.

That all animals derive their food from plants in the last analysis does not impress us as unethical, because we think of plants as without feeling. This sentiment has, however, nothing to do with the point at issue, which is that the whole animal kingdom exists by destroying as much as possible or profitable of the plant kingdom. Unless we imagine that plants were ordained in order to be eaten by animals, we cannot fail to be impressed by the ruthlessness of nature. Some plants have reversed the exploitation. Certain bacteria exist by utilizing animals as their hosts. Owing to the difference in size of host and parasite, it may take many millions of bacteria to destroy the animal host, but the bacteria can multiply at such a rapid rate that within a short time they can produce enough poison to destroy the largest animals. In other cases, where total destruction is not brought about, temporary or permanent injury to the animal may result.

Carnivorous animals have developed adaptations through which they are able to destroy herbivorous animals, and since some of the herbivors are large animals (cattle, sheep), the spectacle impresses us, because we carry over to them our idea of a painful death; but there is nothing in nature herself to indicate that consideration of the pain involved enters into the situation, unless painful experiences make the individual more alert to the dangers ever present. Timidity may be a saving element in the victim, but so is ferocity necessary to the victor. One is as characteristic of living things as the other.

Some years ago the famous and tender-hearted Russian, Kropotkin, wrote a charming book entitled *Mutual Help.* He made a valiant effort, by collecting many anecdotes about animals, to show that nature is often kindly, that animals perform acts of kindliness, and even cherish one another. However fine his intentions, the arguments he used will make most naturalists smile, while many of the anecdotes would do better in a child's fairy book.

While parental care does give a picture of kindliness and self-forgetfulness in a few of the higher groups of animals, even this—however intense for a time—is soon over. Aside from man there is evidence that it extends only over a limited period, after which the offspring are treated as any other individuals of the species. A hen may exhibit devotion to a dozen eggs (or even to the place where the eggs were laid), and spend the subsequent few weeks in finding food and protection and shelter for the young; but the instinct soon wanes and she behaves no differently towards her progeny than towards those of any other fowl.

In man the same relations hold, but amongst civilized races the elementary instincts are overlaid by traditions and customs that extend the maternal and paternal relations throughout life; even here, except in abnormal cases, the extreme protection given to the young is less manifest after they have become mature.

There is a curious fact in this connection which might be called an adaptation. Most animals of the same species live peacefully together—except man and ants. Destruction of their own kind might seem so highly disadvantageous to the species that it would seldom occur, but there are a few cases where animals show little consideration even for their own species.

In truth, nature is neither moral nor immoral, and it is unwise to draw conclusions concerning the ethics of the universe from what we find in the behavior of animals and plants. Our definitions of right and wrong rest on the arbitrary rules man has adopted, supposedly for his own welfare as a social being. How futile, then, to pass judgment on the conduct of other animals according to the rules that man sets up on the basis of his own behavior within his group; and how foolish to attempt to draw inferences as to the ultimate meaning of the universe by emphasizing the widespread selfishness of each species for its own perpetuation, or the rare cases of unselfishness in the individual's behavior within the species.

PROPAGATION AND SURVIVAL

Keeping in mind, then, the lesson that a wider experience teaches—the lesson that the problem of adaptation is concerned largely with each individual for *itself alone*, and is selfishly apart from any grand scheme concerning the beneficence of the universe—keeping these things in mind, and not wishing to introduce a demon whenever things seem to be going wrong, let us turn our attention to a subject of fundamental importance for the theory of natural selection, namely, the propagation of animals and plants; for it is the ability to multiply their kind that is the most distinctive feature of living things as contrasted with the not-living.

It was one of Darwin's postulates that through overproduction, competition comes into play, and through competition survival of the fittest takes place. Darwin argued that, if the adult population remains on the average fairly constant over a period of years, it follows that the rate of reproduction must be just sufficient to maintain the species under present conditions. There is here the implication, at least, that there must be enormous elimination through competition of the adult stages.

If all the eggs laid came through to maturity the number of adults would be a measure of the rate of reproduction. But we know that this is never the case. Sometimes the number of eggs produced is enormous, and the proportion of young that reach maturity may be less than one in several millions. It is said that a salmon may produce 28,361,000 eggs, a turbot 9,161,000, and a cod 6,652,000, a herring 21,000 to 47,000; the queen bee may lay in three years 5,000,000 eggs. The American oyster produces from 15,000,000 to 114,000,000 eggs at each spawning and may spawn four or five times a year. The Japanese oyster produces from 11,000,000 to 55,000,000 eggs at a single spawning. According to Punnett, a rotifer (Hydatina) lays about thirty eggs measuring 0.01 cm. At the end of a year, after sixty-five generations (if all lived), the total mass of material produced would make a sphere larger than the confines of "the known universe." A single infusorian in seven days produced 935 descendants. Another species at the end of thirty days (at the rate of one kilogram in six and one-half days) would give one followed by forty-four zeros, a mass a million times larger than the sun.

"Microbes" have been seen to divide every twenty minutes under favorable conditions. Those in a glass of milk, if multiplying at this rate, would make in five days a mass larger than the earth.

It has been estimated that a dock plant produces 25,000 seeds a year, a horned poppy 75,000, and a mullen plant 700,000. These figures give at least a rough idea of the enormous rate of reproduction that some animals and plants are capable of as long as the conditions of life are favorable.

It may appear, at first thought, that an increase in eggs would give a proportionate increase in the adult population. This would happen, of course, provided the saturation point of food for the young had not been reached, and if there were room enough in the old or in a new environment for an increased adult population. But in the real world an increase in the number of eggs will sometimes tend to increase the enemies of the young. This will soon reduce what had been gained to the original number. It is generally recognized that the sudden increase in the number of insects of a species (due to the removal of some limiting condition, or the discovery of some new opportunity) may be followed in subsequent years by a gradual decrease, due to an increase in its enemies. The enemies will then in turn receive a check. The host species will now be given a chance to recover and regain its old or some new basis. Naturalists of the last century spoke of the balance of nature, meaning that the rate of reproduction of a species and its natural enemies are so adjusted—or so ordained—that each is kept on a fixed basis; the relation of host and enemy had been so beneficially adjusted that each had its rôle to play in the "economy" of nature. But, as we view the situation today, the benefit is one-sided, in favor of the parasite. We are not impressed by the idea that sheep were created for wolves—although we recognize that wolves do destroy sheep. When man appeared on the scene and found that mutton was good to eat, he set to work to destroy the wolves, and to domesticate sheep for his own use. The result was an increase in sheep, but also as great an increase in the slaughter of sheep. The anthropomorphic conclusion might seem to follow that sheep had really been created as food for man, and not for wolves. This fatuous assumption does not satisfy the biologist familiar with a wider range of the relations of living things to each other.

It is important to realize that the rate of propagation is not to be taken seriously as a measure of competition amongst the adults of the species in the struggle for existence. The number of young that reach maturity more nearly equals the number of adults existing, on the average, from year to year, than the number of eggs produced. A truer measure would be the number of adults that succeed in propagating, and further, to what extent their success in this respect is due to mere chance or to the individual differences between them. If we had this information we could speak with more accuracy (if with less assurance) of the rôle of competition in evolution.

If the number of eggs produced cannot be used as a legitimate argument to prove the high rate of competition amongst adult organisms, its significance or adaptiveness is obvious from a different point of view; for it is a measure of the enormous loss that takes place in the young stages. If, as I have said, the process seems wasteful to a high degree, it is to be remembered that it is not wasteful if it is regarded as essential for the maintenance of the species. This may be put in another way by saying that the method of propagation followed by a particular species may be such that an enormous loss takes place; but under existing conditions this may be the only method by which that particular species can, or rather does, maintain itself. The same idea may be expressed in still another way, namely, that the chances are so great that an egg or embryo may not come through to maturity that unless a great surplus is produced the species will die out; or again, that the embryos meet with so many catastrophes along the road that many species would go out of existence did they not produce an enormous number of eggs.

There is still another consideration to be taken into account. Owing to changes in the local conditions in which a given species can establish a foothold, a large number of eggs increases the chance that new localities will be found by a few, at least, of the young. In certain cases this may be a very real factor in the maintenance of a species. The number of eggs in such cases would have no significance in the competition amongst adult forms.

If this analysis is correct, or even approximately so, it serves as a warning against a too ready adoption of this part of Darwin's argument. Whether his theory is really dependent on this argument is another question. But there can be no doubt that the property of organisms to manifold themselves is the essential postulate for evolution.

There are relatively few species where, as in man, the male coöperates in the rearing of the young. This occurs in only a few groups, such as the mammals and birds and a few fishes, the midwife toad, and sea spiders. But in the vast number of species with bi-parental propagation, the sole biological function of the male is the fertilization of the eggs of the female.

There has been not a little speculation on the interpretation of sexual reproduction; and while certain writers seem convinced that their speculations or theories have solved the problem, it has really never been satisfactorily settled.

One of the arguments that has been most widely promulgated is that sexual reproduction, by making possible the mixing of the hereditary materials of the individuals composing a race or species, thereby increases the variability of the species, and that this increased variability is an advantage in that it furnishes the opportunity for evolutionary advances in different directions. This implies that by introducing greater variability a species increases its chances of survival even though, as a species, it increases its chances of going out of existence through competition with the new type. The argument, while interesting, is a hazardous one: it is hazardous because it may seem to imply a purposeful procedure on the part of the species. The argument is less obviously risky if it is intended to imply only that those species which are more variable are most likely to produce new types better suited to the old environment or to a new one. But it should not be overlooked that such a procedure will ordinarily cut down the number of individuals of a species suited to the existing conditions, and thereby endanger its existence if carried out on too large a scale.

The widespread occurrence of sexual reproduction has also given rise to theories of a different kind, called theories of rejuvenescence. Some years ago a French zoölogist, Maupas, found that certain unicellular animals that multiply by dividing, do not go on doing so indefinitely, but that after a time degenerative changes set in and finally the cultures die out. But if, before the end is reached, two individuals come together and conjugate, a new period of activity begins after a time, and a new cycle of divisions is inaugurated. From this evidence the conclusion was drawn that conjugation is essential in order to renew the vitality of the individual. The same idea has been carried over to the rejuvenation of the egg by the entrance of the spermatozoön. Such statements are frequently met with, as though the theory were established instead of being pure speculation. The facts give a very insecure basis on which to establish such a far-reaching conclusion. It is not satisfactory to assume that two organisms exhausted by cell-division could by coming together reëstablish their youth. The theory seems as mysterious as the facts it pretends to explain. Moreover, there is evidence of another kind that indicates at least that cell-division is not necessarily a self-exhausting process. There are some higher plants that perpetuate themselves vigorously, and, so far as we can judge, indefinitely, by cell-division. By means of slips or cuttings some of our cultivated plants are perpetuated without any decline in vigor. Even in the protozoa, and in one of the forms that Maupas used, it has been shown that, by feeding on a more complex or normal diet, no signs of degeneration appear. Woodruff has kept a race of paramecium actively going on for over 8000 cell-generations.

It has been pointed out that there are races of Indian corn that when inbred become weak, but when they are outcrossed their vigor is renewed. In this case it appears that bisexual reproduction through outcrossing brings about recovery from inherent weakness (due to the presence of recessive factors), thus overcoming the bad effects of the recessive factors present by introducing dominant ones. Now, if through mutation downhill changes are of frequent occurrence, it may seem that bi-parental reproduction may be a means of escaping from this situation. In a few generations individuals containing these disadvantageous characters may be eliminated. It is better not to press this argument too far, for we are aware that without fuller analysis of the benefit conferred (which we cannot make at present for lack of data) its validity may not go unchallenged.

Yet on the other hand we cannot afford to neglect any promising lead we may find, unless we are willing to leave the problem of bi-parental inheritance in the mists of ignorance and superstition that have always surrounded it. For there is a great deal of circumstantial evidence pointing to the advantage of this method of propagation, even though it seems to call for twice as many individuals as might seem necessary in order to produce new ones.

The suspicion that bi-parental inheritance may be advantageous is supported by another class of phenomena that is especially prominent in the higher plants. Here each individual produces both pollen and eggs on the same plant—it is both male and female—yet, in many of these monoecious plants there are many devices or ways that assist in or insure cross-fertilization.

The colors of many flowers, as well as their odors, are usually described as adaptations—signals hung out to attract insects that accidentally carry pollen from one flower to the pistil of the next one. In addition to this supposed adaptation there are other more specific ones. The shapes of certain flowers seem to be highly adapted for cross-fertilization; sometimes this relation is so extreme that it would seem to jeopardize the chance of the plant's perpetuating itself at all. It may be argued, then, that some very great benefit must accrue if so great a risk is run; yet the risk may not be, after all, so great as imagined. We have no real data that bear on this question.

Among some of the methods that may seem to have been "invented" to insure cross-fertilization in plants is the not infrequent one of self-sterility. The pollen of some of the higher plants is incapable of fertilizing the eggs of the same plant, but is fertile with most other plants.

Recent work has shown in some cases that the failure to self-fertilize is due to the fact that the growth of the pollen tube down its own styles is slower than down the styles of most other plants. While it is a satisfaction to have detected the immediate cause of self-sterility in these cases, it may seem to leave the question of the origin of the process where it was before. However, recent genetic work has shown in some cases that self-sterility depends on genes that follow Mendel's laws in their inheritance. Such information relieves us of the need to explain how such a condition of self-sterility was gradually evolved. If it seems plausible that such genes appeared suddenly and were discontinuously inherited, a fair case, if not a demonstration, could be made out for its perpetuation, provided some advantage, however slight, would result from cross-fertilization.

It is known that many degrees of self-sterility exist, and following the usual procedure of the neo-Darwinian school, these would be represented as stages in the evolution of complete self-sterility. But as Darwin himself recognized clearly, the argument is fallacious, because any individual showing incipient self-sterility would, by definition, have fewer offspring, and stand a poorer chance of self-perpetuation than its fellows. On the other hand, as stated above, some of the modern work in genetics makes it probable that factors for complete self-sterility may occur at a single step. If, by excluding self-sterility completely, there is a chance, *then already existing,* that cross-fertilization will take place, and if some advantage accrues, the occurrence of self-sterility can be more simply accounted for than on the other assumption that it arose by slow degrees.

While it is evident from what has just been said that much more caution than usually employed is called for in dealing with the relation of propagation to natural selection, nevertheless one outstanding fact should not be overlooked, namely, that the power of manifolding themselves is, by all odds, the most important feature of living things. It is this property that makes it possible for a new type, if it has a survival value, to establish itself in time against the opposing weight of the numbers of individuals composing the species.

CONCLUSIONS

The properties of growth and division have made it possible for extremely fragile forms of matter to escape the disintegrating processes characteristic of the inorganic world. It is owing to these two properties of organic life that evolution has been possible.

Evolution means, however, more than the perpetuation of organic materials that once upon a time came into existence on the earth. More complex forms of life gradually developed which survived not so much because they exterminated the simpler forms, but because they found new ways of existing and perpetuating themselves. One of these ways was the utilization of already existing living things as food, not only simpler organisms but even, as in the case of carnivors, other highly developed animals. The whole animal kingdom, in fact, relies on plants for its existence, and many animals depend on other animals for their food.

Diversification was possible owing in the first place to the different physical conditions present on the surface of the earth, and in the second place to the interrelations of the living forms themselves leading to exploitation of one animal by another in a most complex series of relations.

The human mind attempted at first to account for this divergence by supposing that organic material is of such a kind that it responds adaptively (purposefully?) to new environments, whether physical, chemical or biological. This view seemed to find support in the well-known properties of many living things to adjust themselves within rather narrow limits to their surroundings, which in man—owing to his power of association, memory and speech—has been carried to an extraordinary degree of development. But, as the result of greater familiarity with the methods of propagation of living things, biologists have found no support for this apparently simple explanation of adaptation and divergence of living things. These questions are more fully discussed in later chapters dealing with Lamarck's theory and with metaphysical speculation concerning solutions of the "order of nature."

Another attempt to solve the problems of diversification was Darwin's theory of natural selection. If natural selection is interpreted to mean that the *innumerable individual differences* found in all races, varieties, and species of animals and plants are inherited; and if through competition only those better adapted to the old or to a new environment survive; and if the survivors produce offspring that vary further in the direction of selection, a creative process appears to have been discovered capable of explaining the evolution of life in all of its ramifications. When, however, we attempt to go behind the assumptions in the last statement, we see that one of the basic ideas, namely, that this process of variation would go on indefinitely under the guidance of selection, is open to question. The implication in the theory of natural selection, that by selecting the more extreme individuals of the population, the next generation will be moved further in the same direction, is now known to be wrong. Neither the genetic factors responsible for a part of the initial variability, nor the environmental factors, can bring about such an advance. Without this postulate, natural selection is impotent to bring about evolution. On the other hand, if variations arise, owing to genetic factors (mutants) that transcend the original limits, they will supply natural selection with materials for actual progressive changes. There is here no implication that natural selection itself is responsible for the appearance of new types, some of which may have a survival value, except that owing to the destruction of the less well adapted types room is left for the better adapted. If all the new mutant types that have ever appeared had survived and left offspring like themselves, we should find living today all the kinds of animals and plants now present, and countless others. This consideration shows that even without natural selection evolution might have taken place. What the theory does account for is the absence of many kinds of living things that could not survive, partly because they could not meet the conditions of the inorganic world, partly because they found no new environment suitable to their needs, partly because they were destroyed by other animals or plants, and partly because they could not compete with the original type. Natural selection may then be invoked to explain the absence of a vast array of forms that have appeared, but this is saying no more than that most of them have not had a survival value. The argument shows that natural selection does not play the rôle of a creative principle in evolution. On the other hand it should not be forgotten that Darwin's theory did an immense service in pointing out where to look for the materials on which a scientific theory of evolution must depend.

CHAPTER VI

MUTATION

A MUTANT type originates as a change in a single gene. If the change takes place early in the germ-track several or many germ-cells (gametes) containing the new gene may be formed as a result of the mitotic division of the germ-cell containing the gene; but if the change takes place later only a single germ-cell is affected.

If this gene is *dominant,* the individual from this gamete, combining with a gamete of the original type, will show the character. If the new mutant is now bred to the type, the character will appear again in half of the progeny, and if advantageous, i.e., if one that increases the chances of survival of the individual and the race, it will gradually spread through the race. If the new dominant is neither more advantageous than the old character, nor less so, it may or may not replace the old character, depending partly on chance; but if the same mutation recurs again and again, it will most probably replace the original character. If the new dominant character is a disadvantageous one, it will soon be eliminated.

In respect to a new mutant *recessive* gene, the situation is much the same, but the details concerning the chances of establishment are somewhat different. In a species with males and females, the individual carrying one such recessive gene in one of the germ-cells will at first breed back to the old type if it perpetuates itself. One of its offspring will contain the gene in its germ-cells, but only one new gene in each cell. If it succeeds in producing offspring, by mating with a type individual, half of them will contain the gene, but again only once in each germ-cell. This may go on for several generations, and the number of individuals carrying the gene may increase up to a certain point. These carry the gene under the surface, so to speak. But as soon as two individuals that contain these genes meet, one-fourth of their progeny will for the first time carry a pair of these genes and show the recessive character. The chance of the character perpetuating itself will depend on whether it has or has not a better survival value than the original type from which it came. In this respect the situation is much the same as for a new dominant.*

In the human race there are numbers of recessive genes, widely disseminated, that account for the apparently sporadic appearance in the most unexpected quarters of recessive characters. Their occurrence, if widespread, makes it difficult to eliminate them from a mixed population with a bi-parental method of propagation. It is a question whether, in the human race, it will ever be practical to get entirely free from the undesirable recessive genes that are already present, and whether new ones may not crop up faster than those now present are being eliminated.

THE FREQUENCY OF MUTATION

It is difficult to obtain exact figures as to the rate at which mutation occurs, because many of the mutations may affect the external characters so slightly that they escape attention, and internal effects are even less likely to be observed. Moreover, the mutations that are most significant in the life of the individual may be physiological changes whose first origin can seldom be known.

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* As previously stated, the hybrid or heterozygous form may partake somewhat of the character of both parents. This will be considered later.

In Drosophila, where the mutation process has been most extensively studied, the frequency of mutation has been roughly calculated. If we use only viable mutants, their occurrence is about one in five to ten thousand flies, Over and beyond these visible mutant changes there are lethals which are ordinarily overlooked. Moreover, mutation rates differ in different cultures to such an extent that it is difficult to obtain values that have much meaning. Nevertheless a few general facts are known. The data at hand indicate that certain mutations occur more frequently than others. This is important in relation to evolution, for, given enough time, the recurrence of a favorable mutation, however slight its advantage, insures that it will ultimately establish itself.

In this connection another further fact concerning mutation must be considered. There are a few cases on record where a gene appears to change not at random but into another particular gene. The change from white to red pericarp in corn, once it has occurred, is as permanent as any other genic change. There is a further significant point here. R. A. Emerson has shown that the mutation takes place in only one chromosome at a time—not simultaneously in the two homologous chromosomes. It is difficult to see, if such an effect were produced by an environmental agency, why both chromosomes of the pair are not simultaneously affected.

The discovery that certain genes frequently mutate in definite directions has brought this kind of mutation process within reach of the experimental method. The outstanding clear-cut case of this sort was for some time the gene for pericarp color of maize referred to above. Since then several other similar cases have appeared, notably the reversion of Bar-eye in Drosophila to normal, discovered by May. This case, however, turned out not to conform to the usual interpretation of point mutations, but to be a unique case connected with crossing over.

Several other mutable genes have been recorded. Amongst the recent ones, those reported by Demerec have been carefully worked out, especially those in the fly Drosophila virilis. One of these is known as miniature-a. A fly of this kind with a chromosome pair (X-chromosomes), both members of which carry the genes, gives some flies like itself, some mosaics, and some normal-winged flies. It is interesting to note in passing that all three of the mutable genes found in this species mutate back to normal. Most other cases either show the same relation or else mutate to a dominant gene. Even in Emerson's case of maize, where the gene for pericarp color mutates in two directions—namely: from white to red, or from red to white—the mutation of recessive to dominant is far more frequent than that from dominant to recessive. The same difference is reported for plantain by Ikeno.

Equally curious is the fact that there is a great difference in various mutable genes with respect to the stage at which the mutation most frequently occurs. For example: the gene for reddish, a body-color of Drosophila virilis, mutates at no other stage than the maturation divisions of hybrid females. Similar cases are reported for Plantago, and for the flower color of Pharbitis. On the other hand, the willow leaf character of Pharbitis was found by Imai to mutate two and one-half times more frequently in the maturation divisions than in somatic cells. Emerson had long before reported for pericarp color of corn that the mutability of the gene becomes more frequent as the plantlet becomes older. Demerec found in the larkspur Delphinium that one of the genes for lavender flower color had a high mutability rate in the early stages of the plant, a low mutability in the middle stage, and again a high mutability towards the end of development.

Demerec also made the important discovery that the miniature-a gene in D. virilis can be readily influenced by selection. The change here, he found, was due to the influence of other genes that could be added to or taken away from a given stock by Mendelian procedure, with a corresponding change in the kind or rate of mutability. He explains in this way how the rate and kind of mutability can be changed by selection, and the same explanation probably holds for other types (Zea, Mirabilis, Capsella).

These results are of extraordinary interest to geneticists. They show that some at least of the mutation processes can be approached by experimental methods, and encourage us in the hope that in time we may obtain data bearing directly on the nature of mutation itself, and possibly on the conditions that affect the rate of mutation.

It may be asked why the production of a greater percentage of mutants by X-ray treatment is not an example of a causal effect. In a very general sense, of course, the result may be said to be caused by the X-rays, but in so far as the result is the production of all kinds of effects, it is not specific in the narrower sense as would be the case if one mutant type were produced. Moreover, the same mutants appear spontaneously, as we say, i.e., under conditions where it is improbable that they are the results of radium or X-ray emanations. Until the nature of the effect of X-rays is understood, as well as the causes of mutation in general, it is better, I think, to speak cautiously; but since the results show that mutations can be produced by a physical agent, a strong presumption is created in favor of the view that other physical agents may also produce them. This leaves still open the important question as to whether the mutants that have been contributory to the evolutionary process arise in the same way. At present there are no sufficient grounds for assuming that they have had a different origin.

THE STABILITY OF THE GENE

Behind these problems lies a still more fundamental consideration—the assumption of the stability of the genes themselves. There are two ways in which the constancy or the stability of the gene may be regarded. The gene may be an element (or, if you will, a material body) that fluctuates about an average; or it may be an element that is stable in the sense that a chemical molecule is stable—sugar, or an amino acid, or a protein molecule. If the former definition holds, then a multicellular individual is, so to speak, constant because its thousands or millions of genes of each kind give an average result. But it is a far cry from this assumption to assume that because an egg, or a sperm-cell, arises when one or more of its genes happen to be in a lower or higher stage of fluctuation, this phenomenon would persist through all later divisions of the egg-cell. Such a view could only be the result of confused or insufficient thinking.

If, on the other hand, the gene is interpreted as stable, in the sense that a chemical unit is stable, the problem seems simpler and in accordance with the more general biological idea that the material out of which living matter is composed is chemical material and obeys the laws of chemistry and physics. It is not possible to decide between these alternatives by an appeal to present evidence, since the results as we find them would be practically the same on either view.

Multiple allelomorphs, as was stated in connection with their occurrence, are generally regarded as modifications of the same gene. The gene itself is taken as the unit in inheritance. Recently Serebrovsky has offered a different interpretation of at least one such case concerning multiple allelomorphs of the scute gene. Something like ten to twenty different scutes are known, which differ in the presence or absence of certain bristles on the body (Fig. 39). Serebrovsky inter-

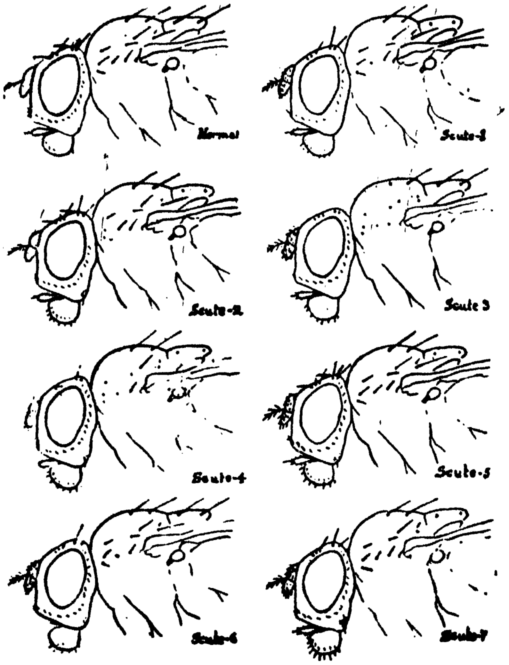

FIG. 39. *Mutant types of scute. (After Serebrovsky and Dubinin, Journal of Heredity.)*

preted each of them as due to smaller parts than the gene—i.e., to regions of various lengths (Fig. 40) that lie at the scute locus. The evidence in support of this interpretation is by no means convincing as yet. The questions involved are under

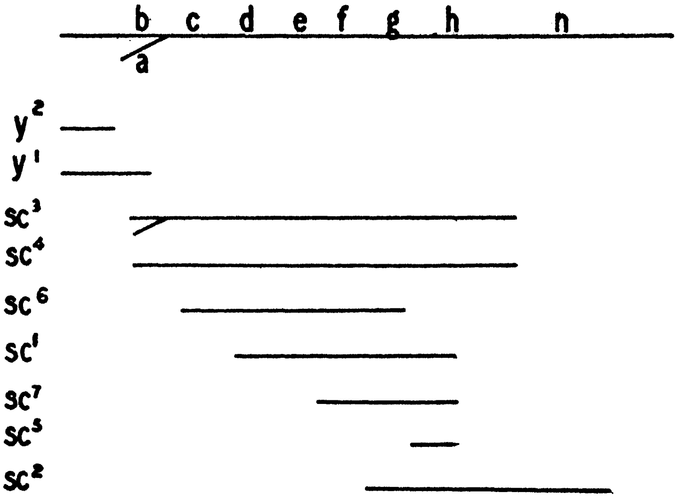

FIG. 40. *Diagram illustrating Serebrovsky's hypothesis of the location of the subgenes at the scute locus. (After Serebrovsky and Dubinin, Journal of Heredity.)*

critical examination, and for the present at least it may be said that the classical idea of the gene as a unit has not been disproven.

DEGRADATION OF GENES

There is evidence that most mutants are no better suited than the original type to the natural environment in which they exist, and not even to any new environment with which we are familiar, if we except the special case of their suitability for work in genetics.

The general picture we get here is of a downhill process: that to a certain extent the germinal material is unstable, and is more likely to go backwards than forwards. This evidence has, in fact, led a few critics of the mutation theory to state that mutants cannot furnish materials for progressive evolution. There are, however, certain facts that weaken this obvious criticism.

In the first place, most wild-types are very highly adapted to the conditions under which they live. Almost any random change is likely to be less adaptive. Second, wherever it has been possible to test by breeding the inherited characters of wild-types, either amongst themselves or with new mutant types, it has been found without exception that they follow the same laws of inheritance exhibited by mutant types which have arisen in pedigreed stock. It is, I think, not unreasonable to infer from this evidence that the characters of wild species have also arisen by mutation. In fact, a not inconsiderable number of wild varieties (elementary species) are known, that differ from one another by a single mutant character.

In the third place, it should be remembered that it is the more extreme, often bizarre, mutants that catch our attention, and, because they are easily picked out, these are most satisfactory for studies in heredity. The smaller mutations, which may be as frequent as the larger ones, or even more so, are much less often studied. It is these, rather than the more extreme sports, that would seem to be more suitable materials for evolution.

We know some mutants that have at least as good a survival value as the original type. It seems, therefore, extremely likely that amongst the random changes appearing by mutation, occasionally one may turn up that is better suited to the old environment or to a new one than the original type.

The study of mutation has revealed another related fact. In a number of species, where the records are on a large scale (Drosophila, sweet peas, maize) the great majority of new mutants are recessive to the wild-type. In other words, the wild-type genes are largely dominant to the new mutant genes. How, then, it may be asked, can we appeal to mutants as the source of new species, if experience shows that recessive rather than dominant mutants are ordinarily produced? This evidence clearly calls for further examination if mutants supply evolution with the materials for new species.

Fisher has recently advanced a theory that attempts to show the tendency for the type gene to become dominant over the mutant as a statistical consequence of natural selection. He points out that there is evidence that many or all of the mutant types have reappeared again and again in the past. These recessive mutants have bred back to the parent stock. The hybrids produced will often be intermediate in some degree, partaking somewhat of the character of the wild-type. Such heterozygotes will be more numerous in succeeding generations than the pure type (homozygote). Amongst these hybrids there will be some that may have met with a gene complex that enhances the dominance effect, and those will have a better chance of survival because of their nearer approach to the wild-type character. In the course of time this may bring such hybrid individuals on a par with the wild-type. When the same mutant appears again, it will now be recessive to the then existing wild-type owing to the change brought about in the stock by earlier occurrences of this mutant, as just explained.

The probability of such a change taking place to an extent that makes it a factor in evolution has been challenged by Wright, partly on statistical grounds. Wright also doubts whether the modifiers for dominance are in general so indifferent themselves to selection that their effect on the mutant change is the main factor controlling their fate. He also raises a further question as to threshold values, if the genes act as catalyzers; and he makes the interesting suggestion that "on the hypothesis that mutations are frequently in the direction of inactivation, and that for physiological reasons inactivations should generally behave as recessives, at least amongst factors with major effects, may be found the explanation of the prevalence of recessives among observed mutations."

J. B. S. Haldane also raises the question whether it is possible at all that the change could come about as Fisher assumes. Admitting that in rare cases the Fisher effect may bring about this result, Haldane thinks that in general the dominant effects are brought about in other ways.

In some groups dominant mutations are by no means infrequent, and are not lethal when homozygous as are many of the dominant mutants of Drosophila. Furthermore, we mean by dominance a gene with reference to the new type; but a recessive gene, if established, might be dominant to other mutations at the same locus (see multiple allelomorphs). The possibility is something like that invoked in Fisher's theory, but less involved.

STATISTICAL PROBLEMS CONCERNING MUTATIONS

The incorporation of new variations into the race in which they have appeared concerns one of the fundamental problems of evolution. If, as many of Darwin's followers appear to have assumed, progressive changes take place by the slow elimination of that part of the population that lies to one side of the distribution curve (which is the same as the selection of those on the other side as the progenitors of the next generation), and if this process goes on steadily and *indefinitely,* then the statistics relating to the resulting changes present one set of problems. But if new types that are inherited—mutations—arise as single individuals and at frequent intervals, an entirely different problem presents itself. The difference in these two situations may be illustrated by a comparison of Galton's laws of heredity with Mendel's. Galton proposed methods for the statistical study of variability in a given population. The methods that Galton proposed have been improved and extended since his time, especially by Pearson and the English school of biometry. Today some of these methods have become indispensable for a preliminary study of many biological phenomena, particularly where the manifold causes of the variability are unknown, as, for instance, in the study of mixed populations, as well as in the handling of numerical data based on chance sampling. By the application of Mendel's laws of heredity many of the problems of inheritance can be studied as specific events referable to known principles. Consequently the Mendelian method has largely superseded the older method, even though we still need the mathematical procedure in cases where the genetic factors have not been sorted out, and wherever we require an exact value of numerical or quantitative data under consideration.

An example may serve to show the advantage of the newer methods of studying genetic variability over Galton's method. In northern Europe and in North America there are many ~~blue-eyed~~ and brown-eyed individuals. It is true that there are other eye-colors, which make the problem more difficult, but these two contrasted colors can be separated from the others and their interrelations studied. Two blue-eyed individuals of blue-eyed ancestry produce only blue-eyed offspring. Similarly two brown-eyed individuals of pure brown-eyed ancestry produce only brown-eyed offspring.

If a blue- and a brown-eyed individual of this kind marry, their children will all have brown eyes. If two individuals that have had such an origin marry, then three-fourths of their children will have brown eyes, and one-fourth blue eyes. The ratio is three to one. The latter, the blue-eyed children, transmit only the factors for blue eyes. But there are two kinds of brown-eyed children in the ratio two to one. Two-thirds transmit factors both for brown and blue eyes, and one-third only the factors for brown eyes. This shows that the factors for eye-color of the grandchildren are in the proportion of one blue to two brown (mixed) to one brown (pure). Mendel's first law gives us an explanation of these numerical relations.

In cases of this kind, the immediate ancestry of the individual cannot be deduced from the eye-color of the offspring. For example: the blue-eyed grandchildren, in the case cited above, have had both brown- and blue-eyed ancestors, yet they carry and transmit only the factors for blue eyes. Similarly some of the brown-eyed grandchildren carry and transmit only the factors for brown eyes, although they have had one blue-eyed grandparent. Conversely, others of the brown-eyed grandchildren transmit a factor both for blue eyes and for brown eyes, etc.

Galton's law of ancestral inheritance does not give us specific information of this kind. It states that one-half of the total inheritance of each individual comes from the two parents, one-fourth from the grandparents, one-eighth from the great-grandparents, etc. Obviously this law does not apply to the present case—at least, not to individuals. Some of the blue-eyed grandchildren in our example do not owe half of their character to their two parents, both of which were brown-eyed. Neither do the hybrid brown-eyed grandchildren owe one-half of their actual eye-color to their parents. Evidently Galton's law does not apply to individuals in a population of this kind. It should be stated, however, that as Galton formulated his law it was not intended to apply to individual cases, but at most only to the average number of different kinds of individuals shown in a large population.

But the law rested on one assumption that may be misleading, namely: that the measurement of a character will serve as an index of past history of the character. Such an assumption may be wrong as applied to character-differences depending on relatively few factors. Whether or not it might be applicable to cases where a particular character is the result of a very large number of conflicting factors is no longer of great interest, now that we know the interrelations of the elements that enter into such a complex problem.

It is sometimes said that, while Galton's law of ancestral inheritance does not apply to cases of discontinuous inheritance, as in the occurrence of blue and brown eyes, yet it applies to cases of *blended* inheritance, and was intended only for this kind of inheritance. Such a statement is not, however, correct.

Students are familiar with many cases in which the offspring of two individuals differing in some character are intermediate (blended) in some degree. In other words, the two characters of the parents blend in the offspring—or, as we say, dominance is incomplete. Nevertheless, Mendel's laws apply with the same force here as in cases where the inheritance is alternate.

It may be claimed that Galton's law is applicable to cases where a number of different factors—some genetic, others environmental—affect the same characters in a plus and in a minus direction, giving a sort of mosaic effect. Size and height furnish good examples, and in fact human stature was one of the subjects that Galton used in his work. There is evidence from several sources showing that human stature is largely due to inherited factors. There are probably several, or many, different kinds of genetic factors that affect the height of man. These have become mixed in so many ways in our present population that it is difficult to disentangle them. Not only may some of these factors influence different parts of the body differently, such as length of legs or back or neck, but in addition there are probably also factors that determine the size and quality of the glands of internal secretion, which in turn affect materially both the rate of growth and the time of cessation of growth. The attempts at present to disentangle the inherited factors in cases of this kind, in order to separate out the Mendelian elements present, are in a very unsatisfactory state. There is, moreover, a suspicion that human stature may also be affected, at least to a limited degree, by the environmental factors during infancy and childhood. Under these circumstances it may seem that the best we could do is to ignore these complications and treat stature as a statistical problem. Such treatment would not furnish readily an analysis of the factors concerned. On the other hand it may be only a matter of time to find out how many genetic factors are present, and then to isolate those that determine growth.

Before leaving the comparison between the two methods of studying heredity, it may be well to inquire whether, accepting discontinuous inheritance and Mendelian laws of inheritance, it would not be possible to *deduce* from a mixed population how many Mendelian units are necessary in order to explain the kind of mixture that is present, and in case two diverse populations have recently come together, how much each has contributed to the existing population. This has been done with some measure of success, especially by the mathematical statistician, Bernstein.

By way of example, the study of a mixed population containing brown and blue eyes may serve our purpose. In certain parts of northern Europe the population is predominantly blue-eyed, in other parts brown-eyed. If the two eye-colors, dominant brown and recessive blue, have lived together for a sufficiently long time, and neither has an advantage over the other, and mating is random, it would be possible to conclude that the mixture was compatible with the assumption that they differ by one pair of Mendelian units.

Conversely, if the mixing of two such races had been of recent occurrence, it might be possible to make a good guess as to how long the mixture had been going on. This would not be, at present, the best way to study genetics, but when certain historical questions come up, such a statistical study may be helpful.

A first-rate illustration of this is found in the distribution of the four human blood-groups. The chief practical interest in these groups is the reaction of the bloods of two individuals when brought together. When certain combinations are made, either in a test tube or when the blood of one individual is transfused into the vein of another individual, precipitation of the corpuscles takes place. If the wrong combination is made the result is fatal to the patient, for the red blood corpuscles are precipitated and agglutinated and stop up the capillaries. Hence, in every hospital where transfusion is practised, great care has to be taken that the blood of the donor does not precipitate the blood of the recipient.

It is not this situation, however, that concerns us, but the proportions in which the four groups are present in different races. Data have been gathered from all parts of the world. It appears that some of the groups have arisen in relatively recent times—after the great dispersal of the human species took place. From a study of the proportions of the types in different races it is possible to make a pretty good guess as to how the mixtures have come about through migration. Not only this, but Landsteiner (1900), Jansky (1907), Ottenberg (1921), and others have shown that the inheritance of these groups can be explained on the Mendelian theory as due to two pairs of genes. More recently Bernstein has shown that three allelomorphic genes may offer a better explanation.

Bernstein has made another venture of this sort. From a statistical study of the human voice, he concludes that the tenor voice of men and the contralto voice of women are due to the same gene; while another pair of genes produces a soprano voice in women and a bass voice in men. This genetic inference is based on the relative proportions in which the voices are distributed in different parts of Europe. Genetic evidence substantiating this view would be obtainable by studying the offspring of parents whose voices belong to one or the other of these categories.

THE MUTATION THEORY AND NATURAL SELECTION

As has been explained, the kind of variability on which Darwin based his theory of natural selection can no longer be used in support of that theory, because, in the first place, in so far as fluctuating variations are due to environmental effect, these differences are now known not to be inherited, and because, in the second place, selection of the differences between individuals, due to the then existing genetic variants, while changing the number of individuals of a given kind, will not introduce anything new. The essential of the evolutionary process is the occurrence of new characteristics.

It is the vague apprehension of this change in outlook that has led to the statement, not infrequently made in popular literature, that Darwinism has been disproved, and sometimes to the more specific allegation that natural selection has been overthrown. The first of these statements need not be taken seriously, but the second calls for further consideration. If natural selection is interpreted to mean the survival of inherited variants, some of which transcend the original boundaries, and some of which show better adaptations than those of the old species or are more suitable to other environmental conditions, then natural selection may appear to offer an explanation of the evolution process. This argument requires, nevertheless, further elucidation. It is true that some variants, due to mutations, do not transgress the bounds of environmental fluctuations. The presence of such mutant factors serves at best only to keep the population at its existing level without producing anything intrinsically new. The more familiar types of mutants transcend more or less the original boundaries, and in consequence produce something really novel. It is also true that mutations appear sporadically and in all, or at least many, directions, and in this regard supply evolution with the kinds of materials that Darwin's theory postulates. More important is the evidence that many mutations have been found to be recurrent. This increases enormously the chance that, if one or more of them should be beneficial to the species, it will succeed in establishing itself.

The real crux of the arguments is the assumption that some, at least, of the mutants will be an improvement, either on the old characters, or in a somewhat different environment. That this may happen, even if only rarely, can scarcely be doubted, because the evidence at hand shows that changes of every sort occur, some increasing, others decreasing the character of parts of the body both structurally and physiologically.

Finally, the strongest argument in favor of the mutation theory is the fact that the only variants inherited are those that appear as changes in the germinal materials. Since the new genes are known to have the power of self-perpetuation, a new beneficial variant may succeed either in replacing the old type or in filling a new place in nature.

Under the circumstances, it is a debatable question whether still to make use of the term "natural selection" as a part of the mutation theory, or to drop it because it does not have today the same meaning that Darwin's followers attached to his theory. Taken at the foot of the letter, we can no longer say that the individual variants, everywhere present, suffice to supply the materials for natural selection; but if it is true, as the mutation theory claims, that small and large variants do appear that are inherited, they would seem to furnish evolution with materials that fulfill its requirements. This question has been considered more fully at the end of the preceding chapter.

More important, historically considered, is the recognition of Darwin's attempt to find evidence in natural processes for the theory of evolution in contrast to the speculative attempts of his predecessors who offered only fictitious solutions of the origin of animals and plants living today. The objective evidence Darwin collected directed attention to the sources from which a solution of the evolutionary problem of biology might be found, and later discoveries have been successful in so far as they followed the same procedure.

CHAPTER VII

THE THEORY OF SEXUAL SELECTION AND HORMONES

THE contrast between the study of evolution by the older procedure and by the newer method of experiment finds an excellent illustration in problems relating to secondary sexual characters. These characters are generally superficial. Darwin attempted to explain their origin historically in his theory of sexual selection, while the modern attitude is to accept their presence as given, and to devote attention to the physiology of their development in the individual. The former theory explained secondary sexual characters, or tried to do so, on account of their usefulness to the individual; the latter theory does not so much consider whether they are useful, but rather tries to explain their development and presence in one sex, and not in the other, as a result of differences in the physiology of the two sexes. These two aspects are not necessarily in opposition, but they indicate the more precise if less ambitious methods of modern work.

Anyone setting out to explain the slight differences that often separate species from one another will soon find himself involved in the problem of the much greater differences that are sometimes present between the males and females of the same species—differences, which even though superficial, are sometimes far more striking than are species differences. Darwin found himself in this predicament. He gave only a few pages in *The Origin of Species* to the secondary sexual differences but devoted to this topic one and a half volumes of his two volumes on *The Descent of Man.*

Darwin's theory of sexual selection aroused more adverse criticism from biologists than did his theory of natural selection. Even Alfred Russell Wallace, co-discoverer of natural selection, refused to believe that the differences between the sexes depended on the choosing of the more attractive male by the female.

In part, the theory introduces an element not present in natural selection, namely, a psychological one; for the result often rests on the assumption of a "choice" of one sex for the more ornamental members of the other sex. It might seem, for this reason, that the theory would make an especial appeal to psychologists and metaphysicians, but the doctrine has received little attention from them. There are two quite distinct sides to the problem. Some of the differences between the sexes Darwin ascribed to a sort of intra-specific natural selection, or competition between the members of one sex for the possession of the other sex. "In the same manner as man can improve the breed of his game-cocks by the selection of those birds which are victorious in the cockpit, so it appears that the strongest and most vigorous males, or those provided with the best weapons, have prevailed under nature, and have led to the improvement of the natural breed or species."

We may leave this aspect of the problem aside, since it is largely a special case of natural selection, and turn to the problem of the origin of those secondary sexual characters which we speak of as ornamental, such as color, plumage, vocal performance, and display. As I have said, Darwin's theory of sexual selection has never been whole-heartedly accepted by evolutionists. Many of the objections advanced have been argumentative, but since the theory itself rests on the same procedure, it is fair to criticise it on those grounds.

A few of the arguments that point to the difficulties of the theory may be very briefly stated. Some of the objections were discussed by Darwin himself.

(1) Since, in most of the species in which secondary sexual differences occur, there are equal numbers of males and females, the question arises as to what happens to the males not selected by the females. So far as the evidence goes, these also usually find mates. Under these circumstances nothing will be accomplished unless other special assumptions are made.

(2) In insects, where some remarkable cases of sexual dimorphism are known, it is doubtful whether the psychic development is sufficient to ascribe to them the necessary powers of discrimination and choice.

(3) The theory of sexual selection contains a hidden assumption which raises another difficulty. It assumes that the female continues to select in successive generations the more ornamental males. This implies that her taste in males, as we would say, steadily advances. But there is nothing in the theory itself to account for this progressive aesthetic improvement.

(4) One of the arguments that has made the widest appeal to biologists is based on the display of the male before the female during courtship. It is sometimes claimed that these antics of the males are of a kind to exhibit to advantage before the female the specially ornamental parts of the body.

A familiar example of this is the strutting of the peacock or the male turkey. Certain spiders are said to pose in such a way before the female that specially brilliant spots on their abdomens can be seen by her. It is indeed a remarkable fact that in some cases the action of the male is such as to lead *us* to suppose the result is purposeful. But there are qualifying circumstances: (a) at the height of the breeding season the male is in an excitable condition, and does unusual and what seem even to us strange things in the vicinity of the female; whether these antics do, or do not, charm the female we have no means of finding out. Many such actions are, or seem to be, futile, and sometimes end in disaster to the male himself, as when the female spider devours a too-ardent suitor. In such cases there is some, though not sufficient evidence that the female when ready to mate will do so with the first male that finds her, whether or not he carries special attractions.

(5) The highly adorned male, especially amongst birds at the breeding season, would seem from the standpoint of natural selection to expose himself needlessly to hawks or similar enemies. Without a very thorough knowledge of the balance between dangers thereby encountered on the one hand, and the supposed advantage in preferential mating on the other hand, it is hazardous to assume that the advantage of adornment of the male compensates for the risk of losing his life.

(6) Darwin appealed in some cases to the theory of the inheritance of acquired characters to help the theory of sexual selection along, or to get it out of special difficulties. Some of his followers have even gone further and tried to explain the over-development of certain organs as a result of use of the parts. Aside from the improbability of the theory of acquired characters appealed to, its application is often

carried to an absurd point, exposing the whole method of dealing with such problems to ridicule.

(7) Darwin sometimes spoke of the more ornamental male as the stronger male, which would increase his chances of mating. This puts the shoe on the other foot, for if his greater strength increases his chance of mating, his adornments would seem to be unnecessary. In fact, as I shall point out later, the same factors that give greater vigor to the male may incidentally be also the cause of his additional adornment. If so, the secondary sexual characters may be no more than a by-product of the same factors that give vigor to the male; hence, as such, are not produced by selective action of the female.

Within quite recent years a body of evidence relating to the development of the secondary sexual characters has come to light that has diverted interest in other directions and perhaps opened a more promising method of approach. This evidence has directed attention away from a discussion that seems rather barren to a field where specific and sometimes quantitative data may be obtained. I refer to the rôle that certain internal secretions or hormones play in the development of the secondary sexual characters.

The most striking differences between the sexes are found in birds where, with one exception (the phalaropes), the male is the more ornamented individual. In the birds of paradise the difference is extraordinary, but the bobolink, the scarlet tanager, and the oriole of more northern species are remarkably different in plumage of the sexes. In the gallinaceous birds, such as the peafowl, the male is highly ornamented. In the mallard duck the male is much more highly colored than the female. In the wild Indian game (Gallus bankiva) the male has brilliant colors and other characters (comb and wattles, spurs, etc.) more developed than the female. Several of the domesticated races of fowls, descendants of this wild species, show similar differences in the two sexes.

It has long been known that removal of the testes of young males of the domestic fowl causes the cessation of growth of the comb and wattles (head furnishings). These organs, while present in both sexes, are much more developed in the male. After castration the comb shrinks in size to less than that of the female. The castrated male, the capon, is also changed in other ways. His sexual instincts are reduced. He seldom crows. It is said that he will take care of young chicks, much as the hen does.

It has also been known to fanciers for a long time that the hen at times may take on the plumage of the cock, and that her comb and wattles enlarge. In many such cases the ovary has been found to contain a tumor, or be in other ways diseased. This happens oftener in older birds. More recently this transformation of the plumage of the female into that of the male has been brought about by the removal of the ovary.

The striking changes in the castrated male and spayed female can be restated in terms of hormones in the following way. The testis of the male produces not only sex-cells, but also, from other cells, a secretion which is absorbed by the blood. This substance, called a hormone (i.e., a messenger), is essential for the maintenance of a large comb and wattles, and for the exhibition of the psychic behavior of the male. The ovary sets free a hormone that inhibits the full development of the plumage and the comb, and affects also the psychic behavior of the female.

The result may also be expressed in another way. The sex of the individual is determined in the first place by the chromosome group that is present. In domestic birds all the spermatozoa have the same number of chromosomes, approximately 50. There are 48 autosomes or ordinary chromosomes, and two sex chromosomes—48 + 2 ZZ. The ripe eggs are of two kinds: half contain one Z, the other half no Z, or 48 + Z and 48. Chance fertilization of the eggs by the spermatozoa gives

Eggs	24 + Z		24
		and	
Sperm	24 + Z		24 + Z
	♂ 48 + ZZ		♀ 48 + Z

Equal numbers of males and females are produced.

In passing, attention may be called to the fact that both males and females contain all the genes, and are alike in this respect, but the female contains only one Z-chromosome, while the male has two. We have come to look upon sex determination as due not so much to the presence of two Zs versus one Z, as to the balance, in the female, between one Z and the rest of the chromosomes; and in the male two Zs and the rest; or, as we say, to a differently balanced relationship in the two cases. This notion of balance is not something peculiar to the sex chromosomes, but is a general conception holding for the interrelation between all chromosomes.

One of the chief characteristics of the male is the development of testes, and of the female the development of an ovary. When the testis has reached a certain size, some of the cells produce an internal secretion that affects the comb and wattles. But the typical male feathers are not dependent on this secretion. They remain unaffected after castration. In the hen the relations are different. Injury to or removal of the ovary, as has been stated, brings about cock-feathering and an enlargement of the comb and wattles, and the growth of spurs. She may even crow, and lose some of her maternal instincts. In terms of the hormone theory, this means that the ovary secretes some substance or substances that normally inhibit the kind of feathering shown by the male. It also inhibits the full growth of the comb and wattles and suppresses the growth of spurs. To sum up: In the female the primary differentiation of sex is determined by the chromosome balance. This leads to the development of the ovary. Later the ovary begins to secrete a hormone that suppresses the fullest possible development of the genetic constitution of the body-cells as seen in the comb and certain feathers of the male.

An important reservation, omitted in the simple account given above, must be made here. There are other glands of internal secretion, besides the sex-glands, that may have a relation to the development of the secondary sexual characters. The suprarenal bodies, the thyroid, thymus, and the pituitary gland at the base of the brain, are organs of this kind. In the operation I have referred to, these glands remained intact, and since present both in the operated birds and the control, may be largely ignored. But since it is known that elimination of some of these glands may cause enlargement of one or more of the others, the problem may well be more complicated than I have pictured it.

Another change takes place after the removal of the ovary that has recently attracted a good deal of attention. In the hen, only one of the two embryonic sex-glands becomes the ovary, the one on the left side. The right organ remains minute, rudimentary and functionless. It was first shown, I believe, by Goodale, that when the left ovary of a chick is removed, the right may enlarge as a round, whitish body, and at times a similar body or bodies may develop at the site of the removed ovary. Benoit showed that this body contains tubules resembling those in the testis. Zawadowsky and Pézard first reported the presence of sperm in these tubules in two cases. Some other experiments had at that time not found sperm in the testis-like body. Later, however, it was found by Domm and others that if the ovary is removed at a very early stage, spermatozoa will sometimes appear in the tubules of the right organ. There can be no doubt, therefore, that a testis replaces the rudimentary ovary, and since the plumage is also male-like, it has been said that a "reversal of sex" has taken place. There is not much use in quibbling over words unless attention is directed away from the real situation; but the term "reversal of sex" is to be used with caution. For instance, it has been said that the female is potentially hermaphroditic because, on the removal of the normal ovary, she becomes a male. Such a statement diverts attention from the real problem. It might be made with respect to any bi-sexual species, since each contains all the genes and has the "potentiality" of the other sex. The male might, in the same sense, be said to be a potential hermaphrodite.

The primary difference between the sexes is a difference in the balance between the sex chromosomes and the autosomes. The real issue, as seen in this case, is the remarkable fact that an individual with the genetic or chromosomal constitution of an adult female, becomes male-like when the inhibitory hormone of the ovary is removed.

This raises a wider question as to the interpretation of the chromosome balance which, under normal conditions, gives males and females. Now this balance should be understood to mean that, in a given environment, the sex chromosome mechanism acts as a differential. Change the environment, and the mechanism may work differently. What we call the environment may be internal or external. For instance, there are several cases in fish where the individual, when young, may function as a male, and later produce functional eggs. Here age may be said to determine whether testis or ovary develops, irrespective of chromosome balance. It is true we do not know in these cases whether a sex chromosome mechanism is present, although in some other fish there seems to be such a differentiating mechanism.

In the male toad there is an ovary-like organ attached to the anterior end of the testis. It is called Bidder's organ and normally does not produce functional eggs. If, however, the testes are removed, the rudimentary organ is transformed after a year or two into a functioning ovary. Here it appears to be the presence of the testes—of some hormone, perhaps—that, working in the same direction as the male sex-mechanism, keeps the male true to type. In the absence of the testis the conditions are such that the rudimentary ovary becomes functional—i.e., is no longer suppressed by the activity of the testes or by somatic influences in general.

In other species it seems that the external environment may change a functional male into a female. In one of the molluscs, the young individuals are females, but if one of them happens to settle down in the vicinity of a large female it becomes a male. Likewise, in the Gephyrean worm, Bonellia, the free-swimming larvae are, to some extent, undifferentiated with respect to sex. If they settle down in isolation they become females; but if one of them settles on the proboscis of a large female it remains small and becomes a rudimentary male—a parasite on the body of the female.

There are some flowering plants with separate sexes, hemp, for example. By treating them in particular ways—especially by regulating the light-hours and temperature—it is possible, in the case of hemp at least, to produce male flowers on a female plant. Here again, even if there is a chromosome mechanism, the sex effect may be altered or supplemented by special environmental conditions.

Other examples could be given but these will suffice to show that the reversal of sex does not deserve the sensational twist that is sometimes given to it; and least of all does it overthrow the theory of a sex-determining mechanism. The way in which this mechanism functions depends on the environment. Those who have studied the mechanism have never made any other claims for it.

The sporadic cases of reversal are, of course, extremely interesting. Their significance lies in exemplifying the principle that sexual characters, like other bodily characters, are determined by differentials, both internal and external, that may act in opposite directions.

In mammals, the secondary sexual differences are not so striking as in birds, but there are still some extraordinary differences. The antlers of the stag or of the moose are the most outstanding cases. At maturity the stag develops his first pair of horns, which may have but one prong. After the rutting season these are absorbed at the base and fall off. The next year new horns grow out, still larger, with one more prong. This process goes on year after year until the older stag or moose is adorned with branching antlers that would seem not only a burden to carry, but to expose the animal to unnecessary danger. Still his greater strength and size enable the stag to survive. Whether horns are attractive to or feared by the female deer is not known. It is sometimes supposed their advantage, if any, is for offense and defense. The males are known to indulge in combat at the breeding season. It does not appear that these combats are often fatal. At most the antlers may be supposed to protect the males against other males. How much weight need be given to this utilitarian argument is uncertain, but there is plenty of evidence that the development of the antlers is dependent on a hormone produced by the testes. The horns develop just before the breeding season, when the testes are enlarging; they are thrown off after the breeding season is over, when the reverse conditions prevail. If a young stag is castrated, the antlers do not develop. If an older animal with horns is castrated, the old horns are thrown off and new ones never appear. The obvious interpretation is that the vigor of the male, excessive at the rutting season, is immediately connected with the activity of the testes. The development of the horns is correlated with the same activity. It is true we do not know that the same hormone produces both vigor and horns, but this seems the simplest view of the facts known to us at present.

In the group of insects there are numerous cases of sex-dimorphism. Some of these are connected with the different rôles of the males and females in reproduction. The female may be much larger than the male, and, correlated with her size, the relative proportion of the organs may be different. The female may be without wings and stationary, even rudimentary, while the male may have wings and be very active.

In insects there is a well-established sex-chromosome mechanism—in fact, two such mechanisms—which are, in a sense, reversed. In some large groups the females have two sex chromosomes (XX) and the male one (X), or an X and a Y. The ripe eggs after reduction each contain one X-chromosome. There are two classes of spermatozoa (X and no-X, or X and Y). This sex-determining mechanism is given in the following scheme:

Eggs	20 + X	or	20 + X
Sperm	20 + X		20
	♀ 40 + XX		♂ 40 + X

In one large group, the lepidoptera, containing moths and butterflies, the reversed relation prevails. The female has one Z-chromosome and a W-chromosome, and the male has two Zs. The ripe eggs are of two kinds, Z and W. The ripe spermatozoa contain each a Z-chromosome. The mechanism is as follows:

Eggs	Z	W
Sperm	Z	Z
	♂ ZZ	♀ ZW

This is the same mechanism as in birds (page 158), since the W-chromosome is supposed to carry no effective genes.

Now when the testes of the young caterpillar have been removed, no changes in the character of the adult take place. The development of secondary sexual characters is not affected. Similarly the removal of the ovary from the female brings about no changes in the markings of the adult (Kopec, Meisenheimer). If the testis of a young caterpillar is grafted into the body of a young female, it continues to grow and produces sperm, although in the absence of the proper outlets the individual cannot function as a male. Conversely, the ovary of a female caterpillar, transplanted into the body of a castrated male, grows and produces mature eggs. Both testis and ovary may ripen normally when both are present in the same individual.

These and other examples that might be given make it clear that in insects there is no influence of the reproductive glands on the secondary sexual characters, or vice versa. In these cases, then, it appears that the same differential that makes the individual male or female, also determines the differences in the more superficial characters. This relation makes the situation somewhat simpler than in vertebrates.

The evidence on which the theory that the sex determining factors give the balance between the sex-chromosomes and the other chromosomes is as follows. It sometimes happens at the maturation division of an egg of Drosophila that both Xs stay in the egg. Such an egg, if fertilized by a Y-sperm produces a female. This XXY female is normal in all respects. Clearly the determination of sex is due to a special combination of chromosomes, and not a peculiarity of the normally male-producing sperm as such.

Occasionally an egg may lose both of the Xs at the maturation division. If such an egg is fertilized by an X-bearing sperm, it develops into an XO male, because the egg has the same balanced relations as the ordinary male. It is evident that the female-producing sperm does not in itself determine that the egg it enters produces a female.

There are also other unusual combinations of chromosomes that throw light on the question of balance. For example: if an egg of Drosophila that has retained its two Xs, as occasionally happens, is fertilized by an X-bearing sperm, an individual results that has three Xs and the ordinary number of other chromosomes. This individual is unmistakably a female, although she is weak and sterile, and has other defects. She is a female because the three Xs turn the scale further in the direction for femaleness. To be sure, the balance is carried too far in the female direction, but there is no doubt as to the kind of result produced.

There are other combinations that change the balance in an individual in such a way that neither a female nor a male develops. For instance, individuals are sometimes produced (from triploids) that have three sets of ordinary chromosomes and two X-chromosomes (2X + 3a). These individuals have characteristics both of males and females. They are mosaics of the two kinds of characters rather than blends of the two sexes. Here the number of Xs is the same as in the female, but there are three sets of autosomes (instead of two) which gives a new balance somewhere between that of the two sexes.

Finally, there are higher combinations of chromosomes where the balance is the same as the normal one, but the total number of chromosomes is different. Thus, there is a tetraploid female with the formula 4a + 4X, in which the balance is the same as in the normal female. This female is exactly like the ordinary female.

These instances show plainly that it is not the number of Xs that determines whether an individual is a male or a female, but the ratio between the Xs and the other chromosomes.

This upset of the balance has also been used by Goldschmidt to explain the exceptional ratios of males to females, and also the occurrence of intersexes in certain hybrid crosses between races of gypsy moths. The interpretation rests on the assumption that the chromosome-balance determining one or the other sex is somewhat different in different races of this species. Goldschmidt has proposed a scheme more or less consistent within itself that covers an elaborate series of crosses. In one series of hybrids the males are transformed step by step into females. In another series the females are step by step transformed into males. These transformations involve not only the secondary sexual differences of color, wing pattern, size, and antenna, but in the most extreme transformations the sex-cells and sexual organs as well.

An examination of these intersexual forms shows that, while some of the characters are intermediate, most of them are mosaics of the two patterns. A further study of the embryonic development in these moths has convinced Goldschmidt that the earlier characters to be differentiated are those of the male; later those of the female tend to come forward. According to the time at which this change takes place, one or the other kind of character will predominate—hence the different grades shown by the different intersexual combinations. The time, then, at which the change in balance begins, will determine whether the intersex is more male-like or more female-like. When the change takes place very early a female may be completely changed into a functional male, or a male into a functional female.

The way in which the organs or characters are determined by the balance of the chromosomes is a matter, at present, of pure speculation. Goldschmidt suggests, as others have done, that the genes may act as enzymes—that is, they are themselves enzymes or produce specific enzymes. This gives a picture of the genes as hormones. He supposes, in fact, that these enzymes begin to function at different rates—the male enzymes beginning before the female in certain crosses, and conversely in other crosses. This explanation may seem to be no more than a description of the results in terms of postulated enzymes, but would be justifiable, whether in terms of enzymes or not, on the basis of a consistent relation running through an extensive series of crosses, as well as by Goldschmidt's examination of the pupal stages of the hybrids. Omitting the enzyme hypothesis as not established by direct observation, it might be said that in certain races of the gypsy moths the balance between all the genes affecting sex determination is more on the female side and in other races on the male side. In the hybrid these relations are supposed to affect the characters in the way he postulates. It is equally conceivable, however, that all the genes may be functioning all the time, the effect depending on the nature of the different organs or on the age at which the genes exert their influence.

In contrast to these intersexes there are other unusual types that are called gynandromorphs, in which one part of the body may be strictly male, another part strictly female. These are interesting as showing that in the insects, at least, male and female characters may exist side by side without any effect on each other. Gynandromorphs are otherwise interesting, as well, because they furnish striking and convincing evidence that the chromosomes are the bearers of hereditary characters.

In birds and mammals this kind of gynandromorph does not occur, and the explanation is at hand. In these forms the sex-glands, as we have seen, take over the rôle of determining the secondary sexual characters. Even if a chromosomal mosaic should appear, its peculiarity would be overcome or obscured by the action of the sex-glands.

The sharp contrast between the older speculative procedure, that tried to explain secondary sexual characters, and the new experimental way of studying the same problem, is evident from what has been said. There is no need to claim that the modern method has solved the historical problem of the origin of secondary sexual differences, but it is clear that the more precise and verifiable work of recent times may in the end help towards a better understanding of one of the problems of evolution.

It may be urged that modern physiological work, dealing with the hormones of the reproductive organs and their effect on the secondary sexual characters, has nothing to do with the problem of the historical evolution of these characters. While this may be true in one sense, nevertheless, in so far as the experimental evidence with birds has shown that it is in the gonads rather than in the brain that the actual change originates, I cannot but think that our outlook on the problem has been altered. If, for example, it could be shown that the same hormones that affect the secondary sexual characters are important in regulating the sexual behavior of the male, which is essential to reproduction, the secondary sexual characters would then be regarded as by-products of the hormones, and would not call for explanation of a different kind.

CHAPTER VIII

EMBRYONIC DEVELOPMENT AND ITS RELATION TO EVOLUTION

ONE of the important chapters of the Evolution Theory concerns the interpretation of the evidence from embryonic development. If, as was held by many biologists for more than half a century, the embryo repeats in its development the history of the evolution of the group to which it belongs, there is placed in our hands the means of unravelling the series of changes that have taken place in the past; and if, as many embryologists piously hoped, this knowledge might in time help us to discover the laws governing evolution itself, we can understand the immense enthusiasm with which this study was undertaken. If the value of a scientific theory is to be judged, in part at least, by its incitement to extensive observational study of a great field of biology, then this theory of recapitulation may be said to have played an important rôle in the history of evolution. For, as a result of interest in the theory, an enormous amount of descriptive work on embryology was published at the end of the last and during the early part of the present century, so that we have a very complete knowledge of the stages through which animals pass from the egg to the adult.

It is also not without interest to recall in this connection that all the great groups of animals known to us were in existence at the time when paleontological history begins. Hence, there are no fossil remains of the ancestors of these forms. In the absence of these we can never hope to get direct evidence of the interrelations of the great groups. It is true that the group of vertebrates has evolved since the lower Silurian, and has left its bones in the rocks. This record gives a picture of the succession of types within the limits of the group, and from this information we may infer the kinds of changes that may have taken place in other groups. Nevertheless, the greater part of the history of the animal kingdom is lost forever, and can at best be only a matter of conjecture. It is not, then, to be wondered at that the theory of recapitulation, which promised to unravel the remote past of all the great branches, attracted the keenest interest at a time when the theory of evolution itself was in its infancy.

If this work seems today to have failed to reveal the past history of evolution, and certainly to have failed to give a causal interpretation of development itself, nevertheless it served another purpose. It furnished abundant evidence that was consistent with the theory of descent, and it was the forerunner of an experimental study of development that has taught us a good deal about the possibilities of the developing egg and embryo. In turn, this work made evident the fact that we knew very little about the chemical and physical events which go on as development proceeds. This lack of knowledge led after a time to a study of the physico-chemical changes in the egg and embryo. It is this kind of embryological research that is being actively pursued at the present time.

When the microscope had reached a stage of perfection that made it possible to see small eggs, the early development of the egg attracted the attention of some very acute observers.

It is not necessary for our present purpose to go into the discussions that arose as to whether the embryo was pre-formed in the egg or in the sperm-cells; or whether development of the embryo takes place by moulding unformed materials into concrete structures. We now know that neither alternative is correct.

CRITICISM OF THE RECAPITULATION THEORY

With this introduction, let us look somewhat more closely into the history of the recapitulation theory. The idea that the embryos of higher forms correspond to the adult stages of the lower forms had been expressed by several earlier observers (Kielmeyer—1793, Oken—1805, Walther—1808, Meckel—1808–11–21), but since, at the time, the relation was not made part of a theory of evolution as formulated today, the resemblance was accepted rather as an interesting fact concerning the plan of creation, without the special significance that it came to have later when the theory of evolution was accepted. Von Baer (1828), who was not an evolutionist, opposed the idea, which some of his contemporaries had proposed, that embryos of higher forms resemble the adults of lower forms, and set up, in place of it, certain generalizations of his own, which in the history of biology are generally referred to as Von Baer's Laws. They may be stated as follows:

1. The most general features of a great group appear in the embryo earlier than do the special features.
2. Out of the most general, the less general structures arise, and so on until at last the most special structures appear.
3. Each embryo of a given adult form of animal, instead of passing through other adult forms, on the contrary diverges from them.

4. Fundamentally the embryo of a higher animal is never like the adult of another animal form, but only like its embryo.

While these generalizations do express certain superficial facts, the implications in them may be very misleading, particularly in the light of more recent evidence that alterations may take place at any stage in the development of the embryo without changing to the same extent (if at all) the end-stages. Such possible falsifications of history show that Von Baer's generalizations may be quite misleading as expressing laws of development. On the other hand, his conclusion, that the young stages are not like the adult stages of animals lower in the scale, but are like the young stages of those animals, is in accord with an idea that has been slowly gaining ground. The young stages may indeed often be "like" the adult structure, but not a repetition of the adult structure. Curiously enough, it was Louis Agassiz, the opponent of evolution in the modern sense, who suggested (1840) that the embryo of higher forms resembles not lower animals of the same group living at the present time, but the adults that lived in past times. This is, of course, what the recapitulation theory, as formulated by Haeckel, really implied, if it is the ancestral stages that are telescoped into the embryo. But Agassiz did not accept the theory of evolution, and his comparisons had no meaning from that point of view. Neither did Von Baer's statement have the meaning that an evolutionist would give to it today.

Darwin accepted the somewhat naïve interpretation of his contemporaries. But one of his statements taken alone—namely, that "community of embryonic structure reveals community of descent"—is supported by abundant evidence. Between 1859 and the end of the century an enormous amount of work was done—to a great extent, as I have said, under the impression that the evolution of animals could be deciphered by their embryonic stages. Phylogenies—family trees—based on this work grew popular, but led to many differences of opinion. For the larger groups, at least, there were about as many phylogenies as there were students of the embryology of these groups. Of its own weight of contradictions the method fell into disrepute, and towards the end of the century was replaced by experimental work, and later, as I have said, by a more refined application of physical and chemical methods.

While it is admitted on all sides today that a strain too great to bear was put on the facts of descriptive embryology, nevertheless hosts of cases were discovered which are contributory to the evolution theory in the sense that they find their simplest interpretation on that theory. The facts almost speak for themselves: the gill-slits found in the embryos of birds and mammals; the appearance of a notochord in the embryo and its replacement by the vertebral column; the sequence of the blood systems in the higher vertebrates; the development successively of head-kidney, mid-kidney, and permanent kidney in the mammals; the embryonic history of the reproductive system, etc. These and many similar facts find their simplest and, I think, a satisfactory interpretation in the evolution theory as representing the past history of the embryonic development of the higher groups.

Take, for example, the group of vertebrates. On the evolution theory, the higher groups have come from species resembling the simpler ones living in the past. If evolution took place mainly in the end-stages of development without greatly affecting the earlier stages, then we can understand why the corresponding embryonic stages in the development of the higher and lower forms are similar.

The gill-slits are a good example. The embryos of the bony fishes develop their gill-slits at a very early stage, while still in the egg membranes. These gill-slits continue over into the older stages, and become part of the permanent respiratory organs of the adult (Fig. 41C). In birds (Fig. 41 A, B) and mammals the gill-slits also develop at a very early stage by the same kind of changes followed in the young fish. Later most of the gill-slits close up and disappear. Two or three of them contribute parts to other organs of the later stages.

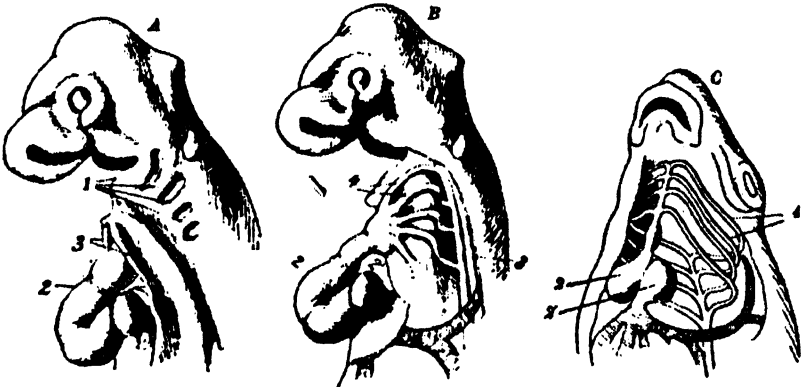

FIG. 41. *Gill-slit and arches, and aortic arches of young bird in A and B. In C the aortic arches of an adult fish are drawn.* (*After Hesse.*)

The whole story involves not only the four or five pairs of slits on the side of the neck, but the aortic arches (included between the slits) that carry the blood from the ventral heart to the dorsal aorta. These arches remain in the adult fish, taking blood to and from the gills, but in the birds and mammals most of them disappear completely, while those aortic arches that remain are incorporated into the circulatory system of the adult. They still carry the blood from the ventral heart to the dorsal side of the body and to the lungs.

This development falls into line with the theory of evolution if we interpret it to mean that some of the early stages of the embryo fish are still retained without much change in the early embryos of the bird and mammal. This interpretation not only satisfies our feeling for continuity and relationship, but brings in no transcendental assumptions, as does the theory of recapitulation, of ancestral adult stages and their condensation into the earlier stages of later forms.

The theory of repetition of developmental stages may at least be used as circumstantial evidence for evolution, because the presence in the young of later groups of the beginnings of a gill-system is in harmony with the interpretation that the later forms have a genetic relationship to the earlier forms as indicated by the presence in both of similar structures. These remain as the essential breathing organs of the fish, but are transitory in the late forms, except in so far as parts of them are preserved and become incorporated in organs having new functions. This single example will serve as typical of many other series known to embryologists.

Lest too much weight be given to this interpretation, it should be pointed out that there is in it no implication that the later or higher forms must necessarily repeat all phases of development of the older ancestral forms. In the course of evolution the embryonic stages themselves may also change and obliterate their resemblance to the corresponding embryonic stages of earlier forms. Many examples could be given where such changes appear to have taken place.

In passing, certain other evidence familiar to embryologists should be mentioned. Here and there in the animal kingdom there are species, and even whole groups, where the reproductive system has matured before the embryonic stages are completed. The later, adult stages are suppressed. The Mexican axolotl is a case in point. The rotifers closely resemble the swimming trochophores of annelids and molluscs; the appendicularian is almost certainly an arrested form of a tunicate. These embryonic stages have become adult sexual forms.

A somewhat similar speculation concerning man has recently been suggested by a Dutch anatomist, Bolk. According to his view, man has not evolved by alterations, especially losses, of the ape-like adult characters of his progenitors, but by suppressing these adult stages. Man in certain respects more nearly resembles the early foetal than the adult stages of the anthropoid apes and monkeys (Fig. 42). Bolk calls this the theory of foetalization. "What is a transition stage in the foetal development of the ape has come to be the end-stage of man."

Bolk supports his view by certain resemblances between the adult structures of man and the foetal structures of apes. The comparisons involve the shortness of the jaw; the partial absence of a hairy covering; the loss of pigment in the skin, hair and eye; the form of the ear muscles; the central position of the foramen magnum at the base of the skull; the relatively greater weight of the brain; the persistence of the sutures of the bones of the skull; the structure of the hand and foot, and several other structures peculiar to man.

I do not wish to present this view as more than an interesting speculation. Whether it will help to allay the qualms of those who dislike to admit an ape-ancestry is doubtful. It doesn't matter much, to my thinking, whether you choose an ape, or the foetus of an ape, as the progenitor of the human race.

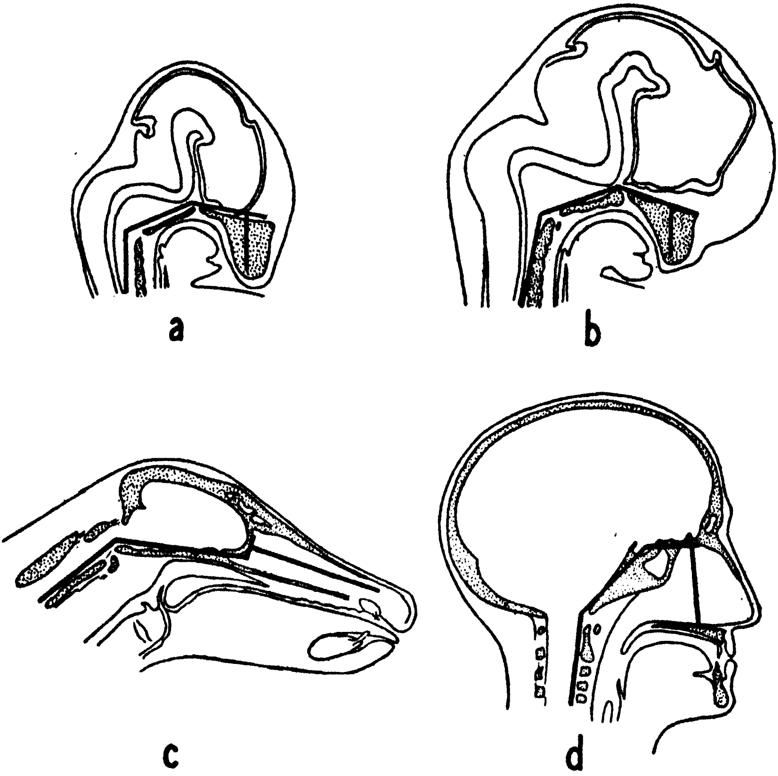

FIG. 42. a *is a longitudinal section through the head of an embryo of a dog;* b *is from a human embryo at the same stage;* c *is from an adult dog;* d *from an adult man.* (*After Bolk.*)

WEISMANN'S THEORY OF THE CONTINUITY OF THE GERM-PLASM

The course of embryological theory was affected to a great extent by Weismann's speculations between the years 1885 and 1896. His name is intimately associated with several ideas that influenced the theoretical outlook of his contemporaries. His theory of the continuity of the germ-plasm became incorporated in embryological teaching. Weismann pointed out that the germ-cells are set aside in the early development as a sort of reserve capital of the race. The other cells of the embryo, the somatic cells, undergo specialization, losing thereby their ability to produce a new whole. Their function is to protect and supply nourishment to the germ-cells.

Weismann's greatest contribution was undoubtedly the idea that the root of all variation was in the germ-cells. In other words, all inherited variation arises first in some sort of change in the germ-cells, although its effects are not unfolded until a later stage in the embryo or adult. It is true, however, that his view that this variability is due mainly to recombinations of the elements received from the two parents is no longer regarded as the primary step, or the only cause of new variants. Nevertheless, Weismann's theory, that we must look to the germ-cells and not to the body as the source of evolutionary changes, has influenced profoundly all later thinking.

Weismann's third contribution was an attempt to explain, on the biological level, how the differentiation of the somatic body-cells in the developing embryo is brought about. His theory is substantially the same as that which Roux proposed earlier. The differentiation of the somatic cells, Weismann said, results from a sorting out of the inherited units or determiners. These determiners are assumed to be carried by the chromosomes, and at each division of the egg the determiners are separated and distributed to different cells of the young embryo. The kind of determiners each cell receives is responsible for its differentiation; stated in the converse relation, the absence of certain determiners in the cells of different regions restricts the possibilities of these cells along definite lines. This was a purely formal hypothesis and stood, even at the time, in apparent contradiction to the well-known fact that at each division of the cell the chromosomes are divided lengthwise into exactly equal halves, so far as our highest microscopes reveal.

In contrast to what was supposed to happen in the somatic cells, Weismann postulated that the chromosomes in the germ-track divide into exactly equipotential parts. Thus, every germ-cell retains the total inheritance of determiners.

It is needless to attempt an elaborate criticism of Weismann's views. The isolation of the germ-cells at an early stage does really occur in many embryos. So far his hypothesis is supported, but in the higher plants the germ-track is so widely distributed in the body that the contrast is obscured. In the lower plants, such as the mosses, almost any differentiated cell may become an egg-cell if isolated.

Weismann's idea that a cell, once specialized, can no longer produce other kinds of tissue-cells has been found to be not always true. For example, the cells of the iris of a salamander may form a new lens when the old one is removed. The cells of the outer layer of an annelid worm may, during regeneration, develop into muscle-cells in the new part. While regeneration of lost parts did often furnish striking examples of Weismann's contention (since cells as a rule do produce like cells), yet so many exceptions were found that it became apparent that some other kind of change than qualitative distribution of determiners must be responsible for embryonic development.

Weismann's theory also implies another kind of isolation, viz., the isolation of the germ-cell from the influences of the somatic cells. This became the foundation of his opposition to the theory of the inheritance of acquired characters.

Today our ideas, based on cytological and genetic work, give a very different picture of development. Since the chromosomes carry the hereditary elements, these are distributed to all the dividing cells of the embryo, whether they are to become germ-cells or somatic cells. Every cell is known to carry all the chromosomes that the egg contains—hence differentiation cannot be determined by the sorting out of their elements. Therefore we are still searching for other factors that bring about differentiation. We can see, at least, that it is initiated by some sort of configuration of the protoplasm of the egg. Furthermore, except in the sense that the germ-cells like all other cells, carry all the hereditary elements, we no longer regard the egg-cell and the sperm-cell as specifically undifferentiated cells. In fact, so far as external structures are concerned, they are visibly highly specialized—even visibly more so at times than many of the somatic cells. The egg, for example, specializes in the storing up of foodstuffs and in protective coverings, and, most significant of all, there is present a configuration in the protoplasm of the egg that determines the course of the early differentiation.

EMBRYONIC DEVELOPMENT AND THE RÔLE OF THE GENES

Let us now return for a moment to the older comparison between the development of the embryo and the evolution of the same animal. The egg often accomplishes its end in a few hours or days, while the evolution of forms living today has taken millions of years. This comparison may give an entirely false impression. The actual changes in the germ-plasm that were involved in evolution may have been thousands of years apart, but each change (mutation) may have taken only a very small fraction of time. The sum total of all these fractions might be less than the time it takes an egg to develop. After each mutation, the egg develops much as before, incorporating or substituting the effects of the new gene into the inherited procedure.

If we regard all evolutionary changes as germinal in origin, the egg of a living species may be said, because of the mutational steps that have taken place, to be as far removed from the egg of its remotest ancestor as the two adults are removed from each other. There may have been originally as many genes as there are at present. Possibly they have been increased, but certainly we have no sufficient grounds for assuming that evolution has been brought about primarily by an increase in the number of genes in the later forms. There may be more genes in higher forms, but we have no way of proving it, and there is probably no need to make this assumption. On the theory that evolution has taken place by a change in the genes already present, the emphasis lies not on numbers but on the kinds of new genes that have appeared.

There is, however, another possibility that should not be forgotten. The genes themselves may be more complex in the later types than in the older types. We have not sufficient evidence to establish this view, but it seems possible that if the later adult forms have a greater complexity of structure and produce a greater variety of substances, some at least of the genes themselves may have become more complex.

Embryonic development consists of a long series of interlocking changes, many of which can be studied by physicochemical methods. These have given important clues to some of the changes taking place. The futility of attempting to decide whether development of the embryo can only be explained by an appeal to vitalistic principles has become apparent from the fact that we are almost totally ignorant of the specific nature of the chemical and physical steps taking place. This is today so obvious that it is not surprising that modern students of embryology have dropped the premature debate, and are turning their attention to the study of embryology by methods that will supply information concerning those causal changes that are discoverable. How far this evidence will carry us we do not pretend to know, but if embryology is to be brought into line by methods that have been successful in other scientific work, there is ample room for a great deal of study in this direction. To point out, as Driesch has done, that changes take place which we cannot at present explain on a machine-theory of development, does not necessarily prove that they may not be physico-chemical in their nature. Such a vitalistic claim could only be convincing if we had a complete knowledge of all the physico-chemical processes that take place in development, and a not-too-narrow definition of machines.

DISCONTINUOUS VARIATION AND GENES

The idea that evolution has advanced by a series of discontinuous steps or stages was originally based on the observed cases of discontinuity in variation of adult characters (Bateson and Korshinsky). Whether this implied some sort of discontinuity in the germinal material was not seriously discussed. In fact, many of the cases of discontinuity that Bateson recorded in his book on the subject relate to somatic changes that would not be inherited, but are the result of changes temporarily affecting the development of the individual. Cases of this sort furnished doubtful analogies with discontinuity based on changes in the germ-cells, and opened the door to a transcendental conception of the evolutionary process, much like the analogies drawn from comparative anatomy.

The idea that lies behind de Vries's theory of mutation offers a very different point of view with respect to discontinuity. The discontinuity de Vries postulates is discontinuity in the elements of the germinal materials. The resulting effect on the characters of the individual may at times present the appearance of a striking change, or may be so slight that the differences between the original and the new character may grade insensibly into each other. Nevertheless, the Mendelian theory of heredity is satisfied with the assumption that a sudden change in a gene covers most of the facts. With the development of the theory of the gene as the basic element in heredity, the discussion of discontinuity has become concentrated on the nature of the changes in the gene when a mutation takes place. From the standpoint of the evolution theory the actual change, whether chemical or physical or something else, is not so important as the inference that, after the change has been made, the new gene represents a new phase of stability. If evolution has taken place by mutation in the gene, the initial steps are by means of a definite discontinuity, in the same sense as a change from one molecular configuration to another is a discontinuous process.

It may be worth while for a moment to follow out the implications in the assumption that evolution has come about in this way. Take, for illustration, the validity of the evidence from comparative anatomy. It is a well-known fact that the theory of evolution has been to a great extent based on comparisons between the adult structures of animals living in the past and in the present, as well as comparisons between forms living at the present time. Paleontology rests its claims on such comparisons, combined, of course, with the known sequence of the appearance of such forms. The comparison between successive stages in the paleontological record seems to imply continuity rather than discontinuity of adult characters. What do we mean, then, by this continuity, if the process has been due to discontinuity in the hereditary elements?

In answer I submit the following considerations. The paleontological comparisons, at their best, involve not a gradual change in one character alone, but the sum-total of all the characters, some of which are almost unchanged, others more changed. As long as a great many characters remain much alike, the theory of common descent is very impressive; but it is, then, not so much the progressive change in particular characters that is impressive as the general resemblance. We are so familiar with the likeness between parents and offspring in man and other animals that we accept without question evidence of the kind. There is, then, a large amount of familiar, factual evidence that appears to justify the acceptance of this interpretation.

On the other hand, the continuity in the advance of particular parts often implied in paleontological comparisons, will appear to the geneticist to be enormously discontinuous—that is, the resultant of many successive mutant changes. Nevertheless, even the sporadic preservation of fossil-remains is consistent with these discontinuous steps, provided it be granted that intermediate types have in the past connected them. It would be hazardous, however, to attempt to draw from the paleontological record as it stands any conclusions as to the single steps in evolution that have taken place.

Genetics has contributed two facts that have a bearing on the recapitulation theory and its modern rival, the theory of embryonic repetition. In the first place, there is abundant evidence that a new gene may bring in a change at any stage of development. In the second place, it is well known that a new gene may change the final stage of development—not by adding something to the end-stage (although this, too, may be possible), but by replacing it by substitution. Both these considerations are worth further elaboration.

We regard embryonic development as an orderly sequence of processes, each process the result of antecedent conditions and a preparation for the following one. Suppose, now, a new gene produces its principal effect on one of these early stages. There are, then, two possibilities: first, that all subsequent stages are affected; or, second, that the effect is, as it were, a side-issue, and later stages are not affected. In the latter case, for example, an organ peculiar to the embryo may be changed, and if the organ takes no further part in the development we can understand how embryonic adaptations may arise that do not affect the character of the adult.

The other alternative is more interesting in its implications. If a new gene brings about a change in an early stage—a change that involves all later changes—it may appear that such an alteration of the orderly sequences that lead to the production of a viable organism would be injurious. Most such random changes would lead to disaster rather than to success. It will also seem that the earlier a change of this kind appears the greater the chance of disaster, and conversely, the later the change the more probably will the complete development be carried out, whether it leads to an adaptive end-result or not.

If this reasoning be admissible, it helps us to understand how it has come about that the earlier stages of development have been so frequently retained, and how evolution has taken place largely through changes in the later stages of development. This speculation gives an historical picture consistent with the preservation of embryonic stages that have, as it were, almost become fixed for a given type of development. It gives at least an objectively rational view of what we find without making an appeal to any other principles than those with which the embryologist and the geneticist are familiar.

CHAPTER IX

THE INHERITANCE OF ACQUIRED CHARACTERS

IT is not as generally known as it should be that the new work in genetics has struck a fatal blow at the old doctrine of the inheritance of acquired characters. The old doctrine held that a modification of the body-cells, produced during development or in adult stages by means of external agencies, is inherited. In other words: a change in the character of the body-cells causes a corresponding change in the germ-cells. A few examples will serve to show how genetics has undermined this already frail and mysterious doctrine.

If a fly (Drosophila) with vestigial wings is crossed to a normal fly with long wings, the offspring have long wings. If these are inbred there are three long-winged to one with vestigial wings. The latter breeds true although its parents had long wings. In other words, the body character (long wings) of the immediate parents had no effect on the genes that produced the vestigial fly in the second generation.

Another example will serve to illustrate the failure of the genes to be affected by the somatic characters of the parent, even when the first generation offspring appears to be due to the blending of the characters of the two parents.

If a black fowl of the Andalusian breed is crossed with a white bird of the same race, the offspring are blue. If these are mated the offspring are one black, two blues, one white. The black and the white offspring (F_2) show no trace of the blending of these two characters of their parents. If the blues (F_2) are inbred, they go on forever giving blacks, blues, and whites. No changes take place in the genes of the blue birds. Hundreds of similar cases could be cited, but these will suffice to show that the character of the parents does not affect the properties of the germ-cells.

If it be objected that, in these cases, the characters are of a kind unaffected by the environment, while the characters transmitted as acquired characters are those so influenced, the following example is significant. There is a stock of Drosophila called abnormal abdomen, in which the segments of the abdomen are irregularly arranged. This irregularity appears, however, only—or very largely—in the first flies that emerge, when the food is fresh and moist. Later-hatching flies in the same culture have only normal bodies. If, now, we breed only from those with normal abdomens, generation after generation, we find that no change at all takes place; the same proportion of flies with abnormal abdomen appear in the first flies that hatch, although the soma of their ancestors has been entirely normal.

One of the favorite arguments of the advocates of the inheritance of acquired characters (a sort of final resort when other evidence fails them) is that effects of this kind require a long series of generations before they become apparent; that one generation, as in the first cases given above, is not enough. There are several answers to this contention. First: the Lamarckians have not hesitated to accept immediate effects of this kind whenever they run across a coincidence that seems to them to be in their favor. The literature is full of such situations. Second: the argument would remove the problem from experimental test—hence the doctrine would have little or no scientific value. But there exist today numerous cases in which it can be shown that no such effects are apparent even after many generations. For example: in the breeding work with Drosophila it is sometimes desirable to make up stocks that carry recessive genes in combination with the dominant genes. These recessive genes may be carried on for many generations in the germ-track of those flies that show only dominant characters. The recessive character can, however, be brought to expression at any time, if so desired, by out-breeding. Two such stocks prepared by Bridges furnish examples of this kind. One, with the formula stubble striped C_{III}, is a balanced stock in which the character striped never appears. This stock was made up seven years ago, and has passed through about 250 generations. Nevertheless, when the character is brought to light, the resulting fly shows that the gene has not been changed. Another such stock, CIIR-plexus-speck over Lobe, also a balanced stock, was made up in 1917, fifteen years ago. At the rate of 25 generations a year it has been carried through about 350 generations without plexus or speck coming out. Yet, when recovered by suitable out-breeding, it has been found that these genes have remained unaffected by the normal soma in which they have been carried.

The history of Lamarck's famous doctrine should not be overlooked in any full consideration of its value. It did not, strickly speaking, begin with Lamarck. In the folklore of many peoples there are stories whose dénouement hangs on this principle. Those who think that, because a doctrine is widespread, it must contain some truth, seem to get comfort out of such arguments. Most superstitions could justify themselves by such an appeal. No doubt a study of the origin and persistence of human superstitions is of value as a peculiarity of man's psychology, but it is hazardous to accept human myths as having any biological value because they have been held widely by people ignorant of the value of critical evidence. As an example of the dangers of accepting popular superstitions, I may cite the so-called inheritance of maternal impressions. This doctrine is so old, so widely held in the past, so readily accepted by untrained minds at present, and so similar in principle to the other doctrine, that it deserves here at least a passing reference. The oldest and most familiar account is that of the trick Jacob played with his father's cattle, described in the thirtieth chapter of Genesis:

"And he set the rods which he had piled before the flocks in the gutters in the watering-troughs when the flocks came to drink, that they should conceive when they came to drink. And the flocks conceived before the rods and brought forth cattle ring-streaked, speckled and spotted."

It was the spotted cattle that Jacob's father said he might have as his own.

There are similar accounts in modern literature where breeders have reported that, at the time of conception, the sight of another animal differently marked from the parents has determined the color, or some other character, of the offspring. There is a fascination in mystery stories of this kind that gives them ready acceptance despite the multitude of cases where no such result has taken place. It is their romantic appeal that causes them to be so eagerly received by the simple-minded.

The doctrine of maternal impressions might be relegated to the limbo of superstitions and ignored by biologists, were it not that it has crept insidiously into our human traditions. Many a poor woman has been frightened by the widespread belief that the sight of some malformed person, or of a serious accident, will affect the character of her unborn child. It becomes a duty of biologists to contradict in the strongest possible terms this damnable tradition.

If we had time to pass in review the many attempts that have been made during the last hundred years to reëstablish Lamarck's teaching, the story would reveal the weakness and futility of one attempt after another—a veritable nightmare of false logic, of insufficient evidence, of mistakes of many kinds, and of sensationalism rampant. But once in a while a serious attempt has been made to put the doctrine to the test. These attempts I shall consider in a moment. But first I should like to say a few words about the inconsequential evidence that has been brought forward.

The crudest cases are those where an injury has caused a malformation of some sort, such as a scar on an individual. If a birthmark appears on the same part of the body of the child, this is cited as evidence of transmission. A closer examination has sometimes shown, as Weismann pointed out, that there is only a remote resemblance between the parental and the infantile defect. It is only too obvious that most of these cases are mere coincidences. If definite connections really exist, we should expect to find abundant evidence of them, considering the frequency of injuries. It is only when, through a coincidence, a child shows a defect in some part of the body where the parent was injured that attention is drawn to the coincidence, which is interpreted as a causal connection.

The complete lack of a limb or a tail in an adult, and a "corresponding" loss in one or more of the offspring is best illustrated by the case of tailless kittens if they happen to be born of a mother who was curtailed. Such cases are on record. But it is known that there is a race of tailless cats, in which the absence of tail is a dominant character. Crossed to a normal cat, the offspring are tailless to various degrees. If a normal female had had, by chance, her tail cut off, and the father happened to be a tailless male, the facts in the case would be sufficiently covered.

Several experiments by Weismann and others, in which the tails of mice were cut off, showed no later effects. It has been said that, of course, no inheritance would be looked for in such cases, since the tail cannot be expected to influence the germ-cells in its absence. The only comment called for by this late defense of the Lamarckians is that such cases have been accepted by Lamarckians as evidence until their inadequacies have been pointed out by experimental refutation.

The direct response of the body to external agents, especially if they seem to be of an adaptive sort, has supplied material for a number of investigators that has seemed to them to show a transmission of the effects to their offspring. It has long been known that the color of exposed chrysalids of certain butterflies is affected by the color of the background on which they pupate. Moreover, since, in a rather general way, the change is in the same direction as the color of the substratum, the effect is said to be adaptive. Quite aside from the latter interpretation, the main fact is well established. The earlier observers made no serious or adequate attempt to find out whether the effect produced in one generation was carried over to the next. Probably the possibility of each individual being itself responsive to its immediate surroundings seemed more significant from the standpoint of adaptation than that it should have its color-characters determined by the chance background of its immediate parent. However this may be, it is clear that the test is not so simple as it may appear at first sight, for if a hereditary element is present, and also at the same time the pupa responds in the same direction to its surroundings, the extent of influence of each may not be easy to detect. Furthermore, the attempt to find a neutral background for the test raises the question as to what a neutral background may be. In the case of black and white, some shade of gray may come nearest to such an intermediate state, but with red and green, or any other colors, the difficulty is not an easy one to meet.

The numerous experiments that Kammerer made with salamanders and other animals are most often cited in the modern literature of Lamarckism. His results, almost without exception, when repeated have been questioned. They are open to the criticism that he did not work with pedigreed materials, and that, in the absence of quantitative methods, his illustrations are subject to conscious or unconscious bias and selection. When the materials themselves are as variable as those used in many of his experiments, it would seem that a complete knowledge of their intrinsic variability is called for before one is justified in their use.

Guyer has carried out a series of experiments with rabbits in which the problem is approached from a different angle. The lens of the eye of rabbits was injected into fowls, where it gave rise to lens antibodies. The blood serum of the fowl was injected into a pregnant rabbit, causing a considerable mortality of unborn young. Of sixty-five surviving young, four had one or both eyes defective, and five others had eyes that were abnormal. The commonest abnormality was the partial or complete opacity of the lens, usually accompanied by reduction in size of the eye. Other defects consisted of cleft iris, displacement of lens, change in color of eyeball.

A similar experiment also gave the same kind of result. In a third experiment the pulped rabbit lens was directly injected into pregnant mothers, leading them to develop antibodies in the blood. Only one rabbit out of eleven produced defective-eyed young. Most of the experiments gave negative results. A repetition by others (Huxley and Carr-Saunders, Findlay) has also been negative.

This raises the question whether, in the relatively few positive cases, there were not present in the stock some rabbits carrying recessive factors for defective eyes. Indeed, such factors have been found by others in different strains of rabbits. The only answer to this criticism is that in other individuals of the stock used by Guyer, no such eye defects appeared.

Guyer found in a few cases that the eye defect is transmitted as a Mendelian recessive carried by the male as well as by the female, and is not due merely to the action of antibodies in the mother and on the young *in utero.*

Sporadic effects of the kind are interesting, but open to the criticism that the experiments were not made with pure-line, pedigreed stocks. The fact recorded by Guyer that the imperfections tended to become worse in successive generations that were closely inbred is, on the whole, not favorable to the interpretation that the hereditary factors were in the first instance induced by the antibodies. In fact, if the antibodies themselves gave the specific results recorded, it is surprising that the results were not more specific. All this suggests at best that some injurious effect was occasionally produced on the germ-cells that may have had nothing to do directly with the antibody element of the blood serum.

Another instance is one reported by Griffith, of the apparent inheritance of disequilibration resulting from the rotation of rats in a cage. Rats were rotated for several months in cages. Some of the young born outside the cage showed irregularities in their gait, and when tested gave a different and specific response according to whether their parents had been rotated to the right or to the left.

Detlefsen has pointed out that the circus movements shown by the rotated rats may have been due to injuries to the internal ear. It is well known that movements of the kind can be induced by aural injuries. He has also pointed out that at times rats are found that show this type of behavior, and that this can be traced to a diseased condition of the ears. These facts show that, unless strains of rats are used for such work that have first been proved free from inherited characters of this sort, the evidence is always open to suspicion. It is true, according to Griffith's account, that rats showing circus movements did not appear in the control, but if such characters are multiple-factor cases, the question of what constitutes a control is more difficult to determine than seems to have been realized. The apparent specific character of the response—that is, the inheritance of right- or left-turning—may be due to inadequate statistical data.

Sumner carried out a careful series of experiments on the effects of cold on white mice, which gave results that seemed slightly positive but too indecisive to furnish definite proof. The mice were not derived from pedigree stock of known reaction to cold.

It is, I think, something more than a coincidence that a good part of the literature of modern Lamarckism deals with the inheritance of defects, either accidental or intentionally induced. Are defects more likely to be inherited than other characters? If they are, the evidence would be of very questionable value for the theory of evolution, especially for those writers who seek to find a purposefulness in the doctrine —a benefit conferred by some useful action.

The risks one runs in experiments of this kind may be illustrated by an incident in one of my own. The red eyes of a female Drosophila were injured by a hot needle. In a few days the Malpighian tubules became a deep red color, and remained so for the rest of the life of the fly. I bred these flies, and in one culture-bottle out of hundreds I found the larvae had red Malpighian tubules, apparently a case of inheritance. But I remembered that I had once seen a larva feeding on the head and eyes of a dead fly, and its digestive tract became deep red. Therefore, I fed some normal larvae on the crushed eyes of flies, and found that not only the digestive tract, but the Malpighian tubules also, became red and that this condition carried over into the adult flies. The conclusion is obvious. In one culture-bottle in which some red larvae had appeared they had fed on the eyes of dead flies. The result was a mere coincidence and not due to the inheritance of an acquired character.

The most plausible way of introducing the subject of the inheritance of acquired characters is to point out the well-recognized fact that use strengthens an organ and disuse weakens it. This argument is based on familiar changes taking place in some of the organs of our bodies, notably in the skin and muscles, and to a limited extent in the bones. For example: when the palms of the hands or the soles of the feet are subjected to repeated pressure, the skin thickens and hardens. This appears to be a direct, purposeful response. It is not known whether the thickening is due to a more rapid multiplication of the cells in the lower layers of the skin, and if this is so, to a direct response, or to an increase in the blood supply. However brought about, the result appears a purposeful response. It is hazardous to generalize from such a case, because there is an upper limit to such thickening, and the thickened skin may really be no thicker than would be normal for man living under harder conditions of life. In other words: civilized life leads to an abnormal or weakened condition. The response may not be due to a "factor of safety" as it has been called, but only a return to the "normal" condition of the skin. Nevertheless, since at birth, before the feet and hands have been used, the skin of the palms and soles is thicker than elsewhere, it has been argued that originally this has been due to transmission from soma to germ-cells.

Now, if the argument be more carefully considered, the supposed relation is found to rest on dubious grounds. We do not know how use thickens the skin. In some way this thickening is a property of highly specialized tissue—one of its functional attributes. How such a response could be transmitted to the germ-cells is by no means apparent. Only by the assumption, as vague as it is mysterious, that the germ-cells somehow reflect any changes taking place in the body, could such a relation be imagined. On the other hand, if, as assumed by Darwin in his theory of pangenesis, the transformed cells in the skin throw off materials that are carried to the germ-cells and there incorporated in the hereditary material, it can only be said that this does not accord with our present knowledge of the relation of the hereditary materials—the genes—and their influence on development. It is not the function of any one set of genes to produce the skin; it develops in response to many or all of the genes. Only the crudest conception of this relation would make it possible to utilize the theory of pangenesis to account for such a method of transmission, quite aside from the difficulty of penetration of the products of the functional cells to the genes, into the nucleus of the germ-cells.

The converse case is the decrease of a part through disuse and the supposed transmission of the change. The degeneration of the eyes in certain cave fishes and of some of the animals living in the depths of the sea, as well as the partial loss of eyes in burrowing animals, such as the mole, or in those living in subterranean tunnels, as do certain larvae and some ants, are often cited as the result of disuse. These cases make an almost irresistible appeal as the direct result of disuse, but this may be putting the cart before the horse, for it may also be true that individuals with weak vision or no eyes could only escape their enemies by living in dark places.

The physiological problem of coördination in the background of some of these considerations should not be overlooked, for it is often not so much the increase in size of a part, but its functional adaptiveness that would make its inheritance an asset for evolution. Lamarck himself, in a somewhat vague way, implied that the functioning of the part lies back of its adaptation, and would be carried over with the change in structure. There has been some dispute as to what Lamarck really had in view, but it is not worthwhile to discuss the implications of this sort in his writings since he had the most absurd notions concerning the part of the nervous system in the functioning of an animal.

Modern physiology gives us a very complex picture of manifold adjustments of many muscles wherever a coördinated movement takes place which also involves the sense organs and central nervous system. Unless we suppose that the complex of factors involved in the simplest adjustment are also carried over into the germ-cells, the improvement in the muscular apparatus would be entirely ineffective. To imagine how such a complicated system could be transported into the germ-cells stretches our credulity to the breaking-point. For example: if rats or mice are trained to go through a maze until they make no mistakes, and if their offspring are also trained, and the training continues for two, three, or more generations, we might expect—on the theory of the inheritance of acquired characters—that each generation would learn to run the maze more rapidly than the preceding one; or possibly the trick once learned would suffice. The experiment has actually been tried by MacDowell on rats and by Vicari on mice, and no improvement took place. Since there are individual differences in the quickness with which the animals can be trained, if these differences depend on a genetic background there is always a risk in such experiments (if made on animals that have not been made genetically pure for such characters) that those that learn fastest will transmit their qualities to their offspring. In fact, Miss Vicari's mice had been inbred in pairs for many generations, which made it probable that her material was approximately genetically homogeneous.

One of the most elaborate of the more recent experiments is that by the psychologist, McDougall, with white rats trained to avoid a runway with an electric shock effect. The rats were dropped into a middle compartment of a tank containing water. In order to get out they had a choice of two exits—one not lighted, which, if they took it, gave them a shock; the other, a lighted runway allowing them to escape without a shock. The table (Table II) shows the effect in successive generations. A very marked improvement was gradually acquired. Although McDougall tried, he says, to avoid the unconscious effects of selection, the results have every appearance of some kind of selection. What kind of change took place is not apparent. There is nothing to indicate that the effects were due to a specific kind of education connected with an escape from water through a choice of exits. Until the kind of change that took place in the rats is more evident, it is not possible to discuss to advantage the outcome of this work.

In contrast to the cases we have just discussed there are a

TABLE II

TANK RATS	RATS	AVERAGE NO. OF ERRORS PER RAT	NO. OF ERRORS OF BEST RAT		NO. OF ERRORS OF WORST RAT
			ERRORS	RATS	
13th gen.	23	68 + (probably 75 +)	30	1	?
14th "	10	80	42	1	102
15th "	10	70	39	1	96
16th "	5	73	39	1	88
17th "	11	46	9	1	147
18th "	22	62	15	1	142
19th "	15	47	12	1	100
21st "	34	37	9	3	74
22nd "	16	36	6	3	89
23rd "	26	25	3	2	71
CONTROL RATS (*unselected*):					
W. C. 1926	17	170	132	2	?
W. C. 1927	10	164	90	1	299
W. C.	22	149	66	3	234
W. C.	37	144	45	2	229
W. C.	10	114	42	1	170
CONTROL RATS (*adversely selected*):					
W. C.	5	215	204	2	229
W. C. (W. H.)	18	166	75	2	241
W. C. (W. H.)	11	134	81	3	196

few others in which it has been shown that the environment acts directly on the germ-cells by agents which, penetrating the body, reach the germ-cells. Such cases cannot be used as evidence of Lamarckian inheritance. Stockard has shown that prolonged action of alcohol vapor not only makes the cornea of the treated guinea-pig opaque, but some of the young may be defective. The eyes of the young may be imperfect in various ways, and it is not only the eyes that are sometimes defective; the young are themselves weak and deficient. In several cases where breeding was possible, it has been shown that weakness and defects may be transmitted to later generations, even by offspring that are themselves normal in appearance, or nearly so. The simplest conclusion from this evidence is that the germ-cells have been injuriously affected by the alcohol absorbed from the blood of the mother, or the germ-cells of the young *in utero* have been so affected. This interpretation is consistent with what is known in general as to the action of alcohol on eggs or developing embryos. The sporadic effects seen in the young, affecting now one, now another part of the body, are consistent with this interpretation. Moreover, it is known that the effects that weaken or cause abnormalities in development in the vertebrates, are more often seen in the defective development of the eyes than elsewhere.

Finally, some of the direct effects of X-rays and radium on the germ-cells, with the consequent effects on the embryo that develops from such eggs, may again be referred to. The partial or complete sterilization resulting from repeated exposure to X-rays has been known for several years. The germ-cells seem to be especially sensitive, and we see these effects when the cells divide. It is not necessary to conclude that the cells are affected by X-rays only at the time of division, but rather that the results of the treatment on the resting cells becomes more apparent during cell-division. The fact that the fully formed spermatozoön is affected by X-rays is a case in point. The results of the injury to the sperm, if not lethal, may not become visible until after the sperm has entered the egg and made preparations for the first division.

It has been shown by cytological work on eggs and other cells that one of the most striking effects of X-rays and radium is on the chromosomes. It is true that the cytoplasm may also be affected, but the effects appear to be less disastrous than those on the chromosomes. The latter have been found either to stick together or to be broken apart. At a later nuclear division an irregular distribution of the chromatin is often observed. A shorter exposure, or a weaker dose, may produce less serious disturbance to the cells and bring about less extensive fragmentation and fusion of the chromosomes. Similar effects on the germ-cells are produced by X-rays which penetrate the body without producing serious effects in it. It is evident that such effects have nothing whatsoever to do with the problem of the inheritance of acquired characters in the sense in which the term has always been understood.

It is somewhat depressing to give so much time to destructive criticism of a doctrine that makes a wide popular appeal. It sometimes seems as if everybody wanted to believe in the inheritance of acquired characters. There is a mystery about it which gives an emotional setting. Yet if we are not to remain the dupes of our emotions, it is part of the rôle of science to destroy pernicious superstitions, regardless of the appeal that they may make to individuals inexperienced in the exacting methods that science demands.

CHAPTER X

THE SOCIAL EVOLUTION OF MAN

WHILE biologists have come to reject the theory of the inheritance of acquired characters by means of the germ-cells, nevertheless they recognize the fact that the human race has succeeded in another way in transmitting certain traits acquired in one generation to the next. There are, then, in man two processes of inheritance: one through the physical continuity of the germ-cells; and the other through the transmission of the experiences of one generation to the next by means of example and by spoken and written language. It is his ability to communicate with his fellows and train his offspring that has probably been the chief agency in the rapid social evolution of man. In the animal kingdom we find many cases in which the young are protected and cared for by their parents. Such beginnings furnish the background out of which has evolved the more complex relation of parents and offspring in the human race, where a prolonged period of childhood furnishes exceptional opportunities for the transmission of tradition and experience.

In no other group of animals is there evidence that the experiences of one generation are handed on to the next, except to a very limited degree in the higher vertebrates. Any advancement must depend on a physical change in the germinal materials, and this may be a very slow process. But in man the power to alter the behavior of the race is possible because each individual begins his life with relatively few inherited instincts, and even these may be rapidly altered by the training he undergoes from birth to maturity. It is the plasticity of man's brain that makes him unique amongst living creatures.

There is abundant evidence that the physical traits of man are inherited in the same way as those of other animals. Of course, there is every *a priori* reason to expect this, since man propagates in the same way as other animals. In hardly a single respect does he depart from the characteristics of the group of mammals to which he belongs.

In human inheritance we meet with examples of nearly all of the kinds of inheritance shown by other animals and by plants. The inheritance of albinism is an example of a completely recessive character. Albinos are reported from all parts of the world. Their sudden appearance may sometimes be due to mutation, but generally the mutation has occurred in the past. The meeting of two individuals carrying each one recessive gene for albinism, gives three normals to one albino. Of the three normals, two carry one gene for albinism. Should an albino marry a normal, all the offspring will be normal, but each will carry one gene for albinism. If these offspring marry normal individuals, the gene will be further spread in the population. In time, two individuals, each carrying one gene for albinism, may meet, and, as we have just seen, will produce three normals to one albino. An individual albino is at a slight disadvantage compared with normal individuals because, in the absence of pigment in the iris, too much light falls on the retina. Dark glasses correct to some extent this defect. Only once in the human race has albinism been established on any large scale. In the forests of Darien there is a human group containing a large number of albinos. Whether this is the same albinism that occurs sporadically elsewhere is not certain. It appears to be another form of the more familiar type.

Blue eyes is another example of a recessive human character. In certain parts of the world this eye-color is a racial characteristic. It is highly probable that the primitive or original races of man had dark eyes. The blue color of the iris is due to the absence of pigment in the outer layer of the iris, so that the inner layer is exposed. It contains a whitish substance which by reflected light appears blue. Probably in those parts of the world where there is much brilliant sunlight, the dark eye is a protection to the retina. At any rate, the blue eye-color first established itself in the more northern parts of Europe. In all other respects blue-eyed individuals appear to be as capable as dark-eyed individuals. We find them competing in the same group without any obvious advantage to either. But there may be more subtle differences that have not yet been identified. It is known that a gene often produces many far-reaching and sometimes subtle effects other than the one we pick out as the most obvious. But he would be a bold man or a fanatic who at present would attempt to ascribe the peculiarities of behavior of blue-eyed and brown-eyed races to a difference in the genes for these two eye-colors.

Only a few strictly dominant mutational changes are known in man. The most striking involves the shortening of the fingers and toes. It is called brachydactyly. A short-fingered man marrying a normal woman produces children half of whom are short-fingered, half normal. The normals never transmit the character. No pure dominants are known, and no cases of two short-fingered individuals marrying. It seems not impossible that the pure dominant is lethal, i.e., if such a combination is formed, the embryo dies before or at the time of birth. There are at least two localities where short-fingered individuals occur, but there is no evidence that the character is spreading.

Another interesting type of Mendelian heredity is called sex-linked inheritance. At first this puzzled even Mendelian students, as it presented the appearance of an exception to Mendel's laws. But with the application of the laws of chromosomal behavior, and especially with the discovery of inequality in the sex chromosomes, sex-linked inheritance turned out to be a confirmation of the chromosome theory and hence can be explained on the same basis as straight Mendelian inheritance.

A few clear-cut cases of sex-linked inheritance are known in man. Color-blindness is the most familiar. Color-blindness is not in itself a defect that is serious, except when the discrimination between red and green is important, as in ship or in railroad signalling. It is not known to be associated with any other mental peculiarity. The next example is, however, a very serious defect. Haemophilia, or failure of the blood to coagulate when exposed to air, owing to deficiency of an enzyme, may cause the death of an individual. Any internal lesions that lead to bleeding may be fatal. The character is transmitted in the same way as all other cases of sex-linked inheritance. The most celebrated cases are those of the late Czarewich of Russia, and the Prince of the Asturias, the son of the former King of Spain.

There are several cases in man where there is evidence that certain kinds of immunity to protein substances, and to other external agents, are inherited, and many more where there is a suspicion that this is true. In this respect the situation is much the same as in other organisms, where the evidence is more satisfactory.

The most convincing evidence of the far-reaching importance of physical inheritance in man is furnished by the resemblance of identical twins. Twins of this kind come from one and the same fertilized egg, and have exactly the same genetic composition. They are always of the same sex—two boys or two girls. As everyone knows, they are so much alike that an intimate familiarity with them is often necessary to tell them apart. Moreover, this likeness continues throughout life, even when they have been reared under different conditions. There can remain little doubt that down to the minutest details our physical characters are due to inheritance.

How far the psychic behavior of identical twins is due to their heredity and how much to their environment is a more difficult problem. There are many stories of the psychic similarities of identical twins, but this evidence when based on hearsay is of little value. Moreover, most identical twins have lived together in the same surroundings. In only a few cases have they been separated in babyhood, and in only a few have their reactions been carefully studied. The evidence here is not entirely satisfactory. In the first fully examined case, that of Muller, the mental tests of the twins were closely similar, but the emotional reactions less so. In three cases recently studied by Newman this was not so evident. Until more cases can be studied and better tests have been devised for measuring such resemblances and differences, many questions must remain in doubt. But there can be no question that we have here placed in our hands an important opportunity for a study of the influence of heredity on psychological traits.

The inheritance of derangements of the mental faculties of man is a very difficult problem, partly because there are few, if any, parallels in other animals that can be experimentally tested, partly because the diagnosis in man is often uncertain, and partly because the environment is a complicating agency.

Anyone familiar with the medical literature must be appalled at the widespread occurrence of these traits in the human race when compared with wild species. It is often said that the protection afforded to weaklings and defectives in communal life helps, or is responsible for, this excess of defectives; they would quickly perish if their existence depended on their own responsibility. While there is no certain evidence to show that man produces new mutational defective types more often than other animals, nevertheless, in so far as mental defects or aberrations are concerned, it is to be remembered that modern life is extremely complex and artificial, so that a slight difference or deficiency at the beginning of the individual's life may become greatly magnified as more and more demands are made on him.

At the other extreme is human intelligence, man's most valuable asset. Is intelligence inherited? There is a widespread belief that it is, and I should be far from wishing to gainsay it. The main difficulty is one of definition. It is commonly assumed that there is one, and only one, criterion of intelligence —that we are speaking always of the same thing when we use the word. In reality our ideas are vague on the subject. The so-called intelligence test that may give a rough estimate of a certain type of reaction, is assumed to be a measure of a phenomenon called intelligence; but it can do little more, in my opinion, than give a numerical value for a certain situation depending on the physiological and mental conditions of the patient at the moment. It also serves to give some clue to his previous experience in the same or related fields, and may furnish an average result of his innate awareness or quickness of reaction. But this averaging of many heterogeneous things has in the past often led to very erroneous conclusions. So far as heredity is concerned, it is a procedure that the majority of geneticists avoid if possible. Accurate work in heredity can only be attained when the diagnosis of the elements of a situation are known. I have no wish to avoid the issue as to whether "intelligence" is inherited. Let me say, then, that superficial experience seems to indicate that in general better brains may be inherited, as are other bodily characteristics; not perhaps in a 3:1 ratio, but as a combination of a few or even many elements. The difficulty, of course, is—aside from our inability to define what is meant by intelligence—that we do not know here how much is due to nature and how much to nurture.

In contrast to his germinal inheritance, mankind passes on from each generation to the next some of the experiences of the race. Beginning probably by simple reactions and imitation, the conservation of traditions must have been, at first, communicated by sounds, then by speech, then by writing and printing, until today there is a mountain of literature in which is imbedded nearly all human experience. While accessibility to the world's literature leaves each one free to take from it what he needs, this has at times been forbidden and even now conventions, prohibitions, bigotry and ignorance restrict the free use of this accumulated wealth. Racial taboos and prejudices are also orally transmitted, and at times may influence the behavior of the generality of mankind to a greater extent than all the wisdom of the ages.

Owing to the twofold method of human inheritance it is hazardous to predict the future course of man's evolution. At most we can try to study, as impartially as possible, the conflicting interests in the situation; for when the two factors come into conflict, as they frequently do, it is not easy to form an estimate of what the future has in store. For example: genetics has taught us how congenital malformations can be most quickly eliminated from the germinal material, or at least reduced. On the other hand, it is obvious that wise human conventions will not permit any such extremely drastic treatment as this procedure might suggest to the fanatically-minded uplifter. The doctrine that all men are born free and equal carries with it the assumption that they be allowed to breed as they will.

Scientific ethics, based on a knowledge of the harm that may be done to future generations by reckless propagation, is not yet strong enough to persuade those carrying injurious traits to desist from propagation. The difficulty is even greater in the case of psychic disorders. There are a few kinds of insanity, such as Huntington's chorea, where the pedigrees of certain families make it practically certain that the background of the disease is inherited. This does not mean necessarily that the brain itself is initially defective, but that its derangement may be brought about by abnormal functioning of other organs of the body.

In many cases of insanity, the diagnosis is still too uncertain to warrant interference, especially when a particular environment is a contributory factor. It has often been suggested that the pressure of civilization itself is too heavy a strain in many cases for certain individuals. If so, the cure may be rather in returning such persons to a simpler life, where they may be useful, than to attempt to breed a more resistant race.

The contrast between the two methods under consideration finds excellent examples in communicable diseases that have been at times veritable scourges to humanity—cholera, smallpox, dysentery, scarlet fever, yellow fever, measles, malaria, grippe, and a long list of other terrors. In some of these cases it might, of course, be possible to produce a resistant strain, but it would be extravagant at the present time to recommend such a procedure. The great scourges that have swept away countless numbers of human beings—the black death, cholera, yellow fever—may have left behind them the more resistant individuals, and, if this resistance was in part transmitted, it may seem that, as a result of the dreadful holocaust, a local racial immunity has been gained. But no one would recommend such a procedure today, because, in the first place, it is extremely doubtful whether much, if anything permanent, would result from the occasional elimination of the more susceptible. The escape of a large part of the population may be due more often to chance or to location than to resistance. Therefore, unless the elimination was continued for several or many generations the gain would soon be lost. In the second place, there is a suspicion that the gain in resistance sometimes observed after a pestilence has swept over a country, is due to a milder or less virulent type of germ that replaces the original one, and if so, the resistance is more apparent than real. We artificially protect ourselves in the case of smallpox by taking on a mild form of the disease, and in a steadily increasing number of other diseases the same procedure is carried out.

It is apparent, then, that here the genetic method is far less efficient than the curative or preventive procedure. The progress of the human race in its battle with disease is one of the greatest triumphs of evolution. It is, if you like, a social evolution, but it is evolution none the less.

Before we determine how far to make use of the methods that genetics has placed in our hands in regulating the characteristics of the human race, it would be necessary to determine first what standard to adopt—whether, for example, to work toward a homogeneous, average, mediocre, stable group, or whether to work for as great a variety of types as possible.

Unless there is agreement on this point, it would be quite futile to set out on such an errand. Who, then, shall determine what standard to set up? What ideal to build towards? A compromise is followed by some of the advocates of the eugenics movement to the extent of sterilizing the imbecile and insane, those with known or supposed inherited defects. The argument that these defectives and their descendants are a menace to society, in the sense that their supposed greater breeding capacity would in time lead to the replacement of the more capable members, cannot, I think, be taken too seriously; but that this defective class would be a perpetual burden to the social group that supports it in asylums and penitentiaries cannot be doubted. There is not much that is novel, however, in the recommendation that these defectives be segregated and prevented from breeding. Confinement has long been in practice. It is here only a question of perpetual confinement or returning them sterilized to the community. A more intelligent understanding of the conditions, both genetic and social, that produce these unfortunate types is much to be desired. While segregation may be recommended on strictly genetic grounds for certain types, on the other hand imprisonment may be at times dictated by the social or political exigencies of a governing group. While this may promote the stability of a particular system it may not be an advantage for the evolution or advancement of another type of individual. Where democracy is the system in vogue, it is often implied that each individual has the same capacity to fulfill every social requirement as has any other individual. A very little knowledge of the composition of the human species dispels such a conclusion as an illusion.

Now, it would seem to be much easier to make rules for a population that was nearly homogeneous than for a population composed of many types of individuals. But from the point of view of evolution it is by no means certain that a stable, comfortable, commonplace group would be as desirable as one in which the greatest possible variability existed. There are at least two arguments that may seem to favor a mixed human population as better serving the purposes of evolution. The first is the genetic advantage; the chance of new combinations would be greater, and amongst these the opportunity for improvement might be expected. The second is social. The betterment of the conditions of life often depends on single, unique individuals—inventors or leaders arising at a time when circumstances offer an opportunity for new discoveries or progress. The far-reaching benefits of such discoveries may be enormously important for human advancement. We usually think of these in terms of material improvements with the accompanying monetary values, but this is only one side of the question. Even more important for human welfare may be the intellectual and ethical and scientific discoveries that our postulated gifted individuals might contribute to human welfare. They might, for example, help us to find out how the evolution of mankind may so continue that the germ-plasm contribution and the social contribution could both be utilized most advantageously in promoting substantial progress.

What has been said so far relates to the improvement of mankind as it exists today. Evolution in the past, however, has meant the appearance of novelties in the germinal material. Now, if the kind of evolution depending solely on the intelligent control of human conditions is not destined to suppress forever the biological evolution through germinal changes, our chief consideration here is to discuss whether biological evolution, if I may so call it, has come to an end with man's advent on this planet, or whether we can make a plausible plea for further evolution of this kind. Despite the apparent conflicts between the two principles that I have just discussed, I think the question is still open. At least there is nothing to prevent our considering it, and least of all there is no necessity for throwing up our hands in despair. Let us look, then, at the question from the biological end.

The plasticity of man's physical, and especially of his psychic nature would seem to allow further development in many different directions. It has been said that man's brain is so highly differentiated that specialization can go no further. On the contrary, it is the very plasticity of the human brain that would seem to make endless additions possible. There is only one danger, viz., that he may stop propagating as a result of social considerations, based on selfishness, fear, ambition, and self-indulgence.

There is very little real reason to suppose that civilized man is becoming physiologically sterile. The process is, in a sense, self-regulatory in so far as sterility depends on hereditary factors; for the later generations will come from the more prolific stocks, good or bad.

Nor is the picture very different if we consider the whole population, rather than some particular caste within it. It is true that, in certain of the older civilizations of Europe, the birth rate has been declining for some time, until in extreme cases increase in numbers has stopped. The causes for this are pretty well understood: deferred marriage and intentional limitation of offspring. Aside from purely selfish motives the restriction seems due to the expense of raising children, and a laudable desire to conserve the health and welfare of the mother, and to give those children that are born the benefit of the best that civilization has to offer. But the danger is that restriction may be pushed too far. The desire to make possible these benefits should be weighed against the possibility that too few offspring increases the chance that the line will run out. If this should be disregarded, nature will step in and hand over the future of the human race to those branches of it where selfishness or an exaggerated idea of the importance of social rank does not submerge the instinct to perpetuate themselves.

These questions have also a still wider bearing when evolution is considered an end in itself. The increase in population has in the past found an outlet in various ways—by improvement of the industrial and agricultural output, or peaceful penetration into countries where the pressure of population is less; or by successful warfare; or by changing the standard of living through a more equal distribution of the necessities of life. Sometimes one, sometimes another of these methods has been followed. In addition, some enthusiastic optimists believe that through the inventiveness of mankind—as in his production of artificial food by chemical means from the raw chemical elements—there are enormous possibilities for the increase in number of the human species.

Without attempting to judge the merits of these different methods to meet population growth, an important question for the evolutionist is whether an increase in numbers alone gives any advantage in the chances of the occurrence of new types that will replace existing ones.

If mutations appear only sporadically, and, so far as we can see, without respect to the condition of life in which a given species exists, the first guess would be, I think, that the greater the number of individuals the greater the chance of something new turning up. But, on further thought, it will be seen that the answer is not so simple; for while it might take a longer time for a smaller population to produce favorable mutations, this might be more than compensated for by the better chances of survival when the conditions of life are more favorable for all individuals. If an intelligent appreciation of the importance of sustaining better types after they had appeared should be in force, a smaller group might have an advantage.

The converse picture is that of a society grown so large that only the barest livelihood is possible for most of its members. Here we can fancy that all the energy and thought of each individual are concentrated on keeping alive. It seems unlikely that much concern would be given to the difficult problem of discovering and fostering new types. If intelligent understanding of the problem is the means by which man is going to direct his future evolution, success seems more likely in a highly organized society limited in numbers.

It may be said that only extreme cases have been selected; that human society at present is composed of many different strata or castes, that leisure is granted to or gained by only a few, and that from this group the intelligent direction of the future will come. This may be partly true, but it is the leisure class at present that shows little concern with problems of this sort, and if its members are not sufficiently interested to look after the future of their own breeding, how can they be expected to become actively interested in altruistic plans for others?

The popular idea of the rôle of natural selection suggests a somewhat different line of argument. One of Darwin's basic assumptions was over-production, but as I have pointed out, over-production may mean no more than that more eggs are produced than there are individuals reaching maturity. If only the same population is maintained—that is, if the same number reach maturity—the elimination is in the embryos or young and only indirectly affects the adults. Consequently selection may bear little relation to the number of eggs laid or of young born. But if not more than fifty per cent of adult human beings are the parents of the next generation, then we really meet with a more difficult situation, for we do not know for certain, in human society, the relative importance to a social group of those who do not propagate. The queen bee is the only member of her community that leaves offspring, yet the other members are as essential to the colony as is the queen. It is possible to exaggerate the importance of overproduction in a social group with its consequent elimination of the unfit, if this be one of the essentials of Darwin's theory. In man the discovery of a new environment or of a new method of utilizing existing conditions may at times play a far more significant rôle than competition. In other words: a new variation may be of great value, not because it beats all its competitors in a crowded environment, but because it has something new to offer, making new possibilities for the welfare of the group.

It is conceivable that when man undertakes to direct the evolution of his race he may blunder badly. It might even be asked why he should meddle, since nature unassisted has brought about the evolution of man. Why not trust natural processes to do all that is possible under the circumstances? This may or may not be good advice. But let it not be forgotten that man by his ideals as well as by his blundering and selfishness and lack of social consideration, is now determining his future by active interference for good or evil with the course of nature. He may not be able to map out his future, but he has shown at times an astonishing power to interfere with what is taking place.

CHAPTER XI

EVOLUTION AS A RESPONSE TO "THE ORDER OF NATURE"

IT is with a good deal of hesitation that I venture to discuss the causal aspects of evolution as a response to the order of nature, because the term "order of nature" has manifold meanings that suggest different things to different people. To some philosophers it appears to have a mystical meaning, to be a sort of personal deification of the Cosmos; to others it suggests an inherent lawfulness in nature that has an ethical or teleological content. On the other hand, it may be no more than an inference based on human experience. Eddington states that "There can be no living science unless there is a widespread instinctive conviction in the existence of an *Order of Things*, and, in particular, of an Order of Nature." Again: "Science has never shaken off the impress of its origin in the historical revolt of the late Renaissance. It has remained predominantly an anti-rationalistic movement, based upon a naïve faith. . . . Science repudiates philosophy. In other words it has never cared to justify its faith or to explain its meanings." It seems to me desirable to avoid in this connection the use of the words "instinctive conviction," as well as the implied need of justification by philosophy, and to define the order of nature to mean no more than that it has been found possible to formulate certain general principles to account for many of the phenomena that reach us through our sense organs. These principles are largely those that have been tested by experimental methods—the acid test by which scientists distinguish between those generalizations that may by themselves seem logical or consistent and those that have not only these attributes but in addition have been tried out in crucial situations. Whether the world is orderly or chaotic does not, then, matter so much as does our ability to reduce its manifold activities to simple statements. Experience teaches that these formulations enable us to reach conclusions consistent with what we find, and from which we can safely predict with a high degree of probability what will occur in a given situation.

As used by most scientists the concept that nature is orderly is derived mainly from the success with which astronomy, physics, and chemistry have used this interpretation as a working hypothesis. We also take this much for granted in our workaday business with the world about us. But when we attempt to carry over this last conception into the realm of living things we find no common agreement amongst scientists, philosophers, metaphysicians, and theologians as to the meaning of the order of nature. We shall therefore have to go warily over the ground, keeping the discussion as close as possible to biological evidence. It should be added that by "the order of nature in the living world" I mean large-scale processes that take determinism for granted, because so far as the evidence goes we are dealing with phenomena of this sort. It is not necessary to discuss whether a different analysis may some day oblige us to resort in part to small-scale phenomena that include the concept of indeterminism or the uncertainty principle; but to find in this theoretical idea the grounds for an appeal to metaphysics seems to me a futile attempt to obfuscate the kind of problems with which biology has to deal.

At the beginning of the nineteenth century four great French zoölogists laid the foundations of the theory of evolution: Buffon, Cuvier, Lamarck and Geoffrey St. Hilaire. It is true that only two of them, Lamarck and Geoffrey St. Hilaire, promulgated the essentials of the theory of descent, while Cuvier opposed them. Nevertheless, Cuvier's work on comparative anatomy and paleontology supplied material that in the end indirectly contributed to the evidence for evolution. The theory of the descent of living forms from those living in the past was clearly stated both by St. Hilaire and by Lamarck. France was at that time the intellectual centre of progressive work in biology, and these four men occupied a prominent place in their field. Moreover, each had a wide knowledge of the animal and plant kingdoms, and their conclusions concerning the theory of descent were largely based on a great deal of objective information. It seems strange to us today that their advocacy of the theory of evolution had so little influence outside of France. Only after fifty years did the rest of the world become actively interested in the theory of evolution, and the new impetus came from an empirical approach rather than from a rationalistic one.

In addition to the arguments in favor of community of descent, St. Hilaire speculated about the causal aspects of evolution. "The changes in organisms," he said, "result directly from the changes in the environment. These changes may be fortunate or disastrous, and in either case influence all the rest of the organization. . . . If these changes produce injurious effects, the animals so affected perish, and are replaced by others somewhat changed and changed to suit the new conditions." This quotation is frequently cited as an anticipation of Darwin's theory of natural selection, but it should be noted that it differs in one important respect from Darwin's view: St. Hilaire appealed to the environment as producing its effects directly on the organism, while Darwin appealed, in the main, to chance variations as supplying the materials for evolution. Chance variations were supposed to be in all directions, however caused, and always present.

In support of his view, St. Hilaire appealed to the monstrous embryonic forms that so frequently appear. This theme was one of his hobbies, and the emphasis he laid on it probably had much to do with the neglect of his views. He appealed to abrupt changes, somewhat as we do today to mutations; but we now know that the malformations and embryonic monstrosities referred to by St. Hilaire are not inherited, while the chief characteristic of mutants is that they are inherited.

Lamarck, who was St. Hilaire's contemporary, had also promulgated a quasi-causal theory of evolution. He emphasized not so much changes in the environment as the internal changes in the organism itself, by which the animal better adjusts itself to environments already existing. Lamarck, as we have seen, based his theory on the well-known fact that through use we increase the power of performing certain actions that may or may not be beneficial. Conversely, a part of the body may decrease through disuse. As I have pointed out, his theory has failed because his assumption that such changes are transmitted to the next generation has not been confirmed.

Aside from the question of inheritance, the property of organisms to make functional adjustments may not be ignored in our present consideration. For even granting that there is no sufficient evidence that such effects are directly transmitted from the part of the body affected to the germ-cells, nevertheless, as a potential property of the organism, this power of individual adjustment, or self-regulation, has sometimes been regarded as the most unique feature of life. Two examples will serve our purpose. The ability of an animal to produce antitoxins against poisons introduced into the system may save its life. Wherever such potential responses are present they are an advantage. In such cases the newly acquired resistance may not itself be transmitted, but the power of adaptive response is at least an attribute of each organism to meet many kinds of invasions. It is this specific ability to meet such contingencies that impresses us, especially when we find a reaction of this kind to particular substances which the organism can rarely have met. It is customary to argue that this property has resulted from the survival of those individuals which possess such power, and of course this may sometimes have been the case; but so widespread are occurrences of the sort that we must admit the survival argument may seem somewhat strained to meet them. The reaction looks more like a general response and there is more than a suspicion that each reaction is a specific chemical reaction of the protein materials of the animal or plant to a foreign body. Moreover, even if it be supposed that this resistance has been acquired through survival, we must still postulate its existence in some individuals at the start. Its presence even in a few individuals would suffice as an illustration of a response to the order of nature.

The second illustration is also familiar. An animal may learn by experience to adjust itself to a wide range of external agents. This is a response through which the chances of survival of the individual are much increased. In everyday language, we say that a burnt child fears the fire, meaning that agents which cause harm or injury are avoided after the first experience. Conversely, those that give pleasure, or meet a need, are repeated. Through experience with the environment the individual adjusts itself to its own advantage—i.e., it increases its chance of survival. Adjustments of this sort may be carried a step further by a double association which Pavlov calls the conditioned reflex. Of two simultaneous associations, only one of which calls forth a physiological response, the other not, one may be omitted after a time, and the different one will call out the reaction characteristic of the first. For example: a dog that has been fed on meat will secrete saliva when he sees it. If, now, a bell is sounded each time the meat is presented, after a time the sound of the bell alone suffices to bring about the secretion. Extremely complex types of behavior may result that would be quite baffling and even mysterious if suddenly met with, did we not know the conditioning that had built them up.

The first point here that interests us is that the central nervous system of vertebrates, and especially the human brain, is an extremely plastic organ—one which is not fixed at birth for a set type of behavior, but is capable of responding to the order of nature to an extraordinary extent. In teleological language, this type of reaction is purposeful in preserving the individual and thereby perpetuating the race.

The second point of interest is that the system is of such a kind as to meet the conditions of the external world in which the animal exists. While the initial responses are limited, they are closely related to the order of nature; i.e., they appear to us to be such that the animal or plant falls into line with the orderly processes characteristic of the world around it. It is the interlocking of these two systems that impresses us. By the mystic it is accepted as final—not to be explained in the way we try to explain everyday experiences as cause and effect. To the biologist it is a problem, at present partly beyond his reach, but which he hopes to solve, in part at least. To the evolutionist it is a phenomenon that has gradually arisen.

Given the power of reproduction and variation, he claims that such a system, by increasing the chance of survival of living materials, has come about by natural processes. He is obliged to leave it at that.

The last example is brought forward to illustrate the property of organisms to respond adaptively to a wide range of conditions in the outer world. Such a system seems to have great usefulness on account of its pliability. It is true that the same end is accomplished by individual species in another way by systems limited to specific events, such as we see in the instinctive types of behavior of animals. The bee with a minimum of wax makes a comb with the maximum of storage space for honey. The spider makes a web of almost invisible thread, yet strong enough to hold a large insect. The bird builds a stable nest in a most precarious situation, in which its eggs are laid and its young reared.

The flexible system has also its limitations, for the animal only learns after an experience which may be fatal to it. In man, the training of the young forestalls this danger to the inexperienced, and appears to be a further improvement of very great benefit to the race.

We might attempt to rationalize the advantage of this more plastic system by saying that its very power of adaptability for each individual insures a wide range of adjustment. In instinctive behavior we find the reverse situation. The very first response is adaptive, but such reactions seem restricted to relatively fewer situations, and to have little latitude when new situations are to be faced. Both systems exist, and since both succeed it may be well not to claim that one is better than the other.

All this leads up to questions often asked, especially by those who are unfamiliar with the field of biology: Why may not the germ-cells themselves react favorably to the environment, and in this way bring about adjustments to the external world? Why should this property be restricted to the nervous system? Why not make such a recognized property of differentiated living things the causal basis of evolution? Lewis, the eminent chemist, for example, belabors biologists for not accepting so obvious a solution of their difficulties. Let me try in a few words to state why we cannot accept so easy an answer. In the first place, it cannot be too often repeated that, in the majority of cases where a body tissue or organ responds adaptively, it is merely carrying out to a somewhat greater degree than usual its ordinary function as a specific organ. It responds because, as we say, it is *differentiated* already to respond in this direction—as when a muscle enlarges through use; or the skin darkens on exposure to light; or after the removal of one kidney, the other kidney does double work, etc. We do not find that when the skin darkens all the other organs of the body darken. Neither do all the muscles enlarge when one set does. Why, then, need we suppose that the germ-cells should respond? Obviously the expectation would never have occurred to a biologist familiar with the methods of response of differentiated cells. If in reply it be said that the germ-cells being unspecialized, they alone of all the cells of the body might act photographically, the answer is that they are not unspecialized, but highly specialized cells—eggs or spermatozoa. If it be implied that the germ-cells react, as assumed, because they contain all the potentialities of the complete organism in their full complement of genes, the answer is that every cell of the body has the same complement.

Another questionable relation is overlooked when an appeal of this sort is made to the germ-cells. When the egg develops it passes through a long and orderly series of stages which flow, as it were, out of its organization, specialized as it is for this particular series of events. An almost countless series of divisions of the genes, and an elaborate sorting out of cytoplasm, and changes in the chemical composition of its materials are taking place. To suppose, then, that the germ-cells "remember," through all these changes, some trivial incident in the life of the parent from which they become separated as eggs or sperm-cells, seems like an appeal to magic rather than to reason.

In more recent years Henri Bergson has made an ambitious attempt to solve the problem of the response to the order of nature. In his marvellously acute book entitled *Creative Evolution,* he develops as his major premise the idea that adaptive response is a fundamental property of living matter—its chief characteristic, in fact. But if one stops for a moment to consider the vast variety and intricacy of the adaptation of organisms to the external world and to each other, and also the no less marvellous adaptations of the parts to one another, Bergson's assumption means little less than that the attribute of omniscience is assigned to living matter. Living matter is with a gesture endowed with all the omnipotence of the eternal gods. It should not be forgotten that, while the assumption is conceived as a general principle of nature, it is purposeful only in a selfish sense. It concerns itself with a benefit to the reacting individual which may be a catastrophe for many other organisms. Of course, I realize that this is beside the mark, since no claim is made that the *élan vital* is a cosmic moral agent, in the human sense. But unless the destructive principle involved is emphasized, many a soft-hearted reader may be misled into supposing that the vital spirit is the good angel of evolution.

It may seem a far cry to inquire whether natural selection might in any sense be looked upon as an agency in the order of nature. If we start with the assumption that the adjustments of animals and plants to their surroundings are the results of the survival of those individuals most likely to survive and leave their quota of offspring, it may appear that natural selection is *par excellence* an agent that accounts for what is observed. But the implication turns on the meaning of the word *agent.* In using such an expression we may seem to personify nature as though she were an active natural agent directing the course of evolution, or at least of determining—choosing, if you will—what is needed for her ends. By this sort of personification, natural selection might be supposed to be the order of nature concerned with making adjustments between living things and the environment, and between living things themselves. To some biologists natural selection really seems to mean this. But only by a perverse use of the term could natural selection be interpreted to mean an active agent in nature. It is only too easy to forget that the words are used metaphorically. Natural selection is only a generalization combining many facts of observation and a theory as to how these facts can be accounted for by an appeal to natural processes.

Darwin attributed the origin of new variations to chance. He was careful to explain that by "chance" he meant only a large number of unknown causes. In doing so it is evident that he meant natural causes and not mystical or metaphysical agents. Perhaps this was one of the reasons why his theory seemed to some of his contemporaries to furnish a scientific explanation of evolution, and to others to be a dreadful heresy that excluded teleological explanations of life.

The mutationists face the same situation today when they attempt to account for the origin of new variations. They have made efforts to produce specific heritable variations with an adaptive relation to the external agents that called them forth;

but so far without success. This raises the question whether the mutational changes are due to molecular events that are strictly causal, so far as the germ-cell change is concerned, and if so, what relation such changes have to the order of nature. If we assume that the kind of alterations taking place in the materials concerned with heredity (i.e., the genes) are chemical in nature, the mutational changes would be not chaotic events in the ordinary sense, but specific events that are at each step determined by the chemical constitution of the hereditary materials in the germ-cells. If we reject the assumption that some unknown agent, such as a directive principle, regulates all chemical changes, we are forced to assume that it is the rare combinations of events that bring into existence such new molecular configurations. The infrequency of such mutations means no more than that such combinations of events seldom occur. Only in the sense that they are rare do they appear to us to be due to chance. But by laying all emphasis on the importance of the materials in which the change takes place, we get a picture of necessity rather than of chance. This, I take it, is the view that a mechanist would adopt as his working hypothesis. Further than this he would probably not like to go unless he were philosophically inclined—in which case he would probably call attention to the extraordinary coincidence that such mutations, being limited, yet have sufficed to bring about the innumerable varieties of evolutionary changes. He would then, no doubt, claim that there must be some sort of ultimate, pre-established relation between a specific internal molecular order and the order of the external world.

This is little more than a re-statement of the problem from the point of view of imaginary chemical reactions. It is at best only a point of view, not a solution, except in so far as it implies that there are possible relations, between the factors that bring about some of the changes in the gene and the aftereffect of such changes in the organism in its relation to an existing environment. The opposite interpretation would be that the causal change belongs to a category that is not in itself purposeful, even though, after the event, the end-result may seem to us to have fulfilled or discovered a "purpose."

In this connection it may be profitable to recall Lawrence Henderson's discussion of the fitness of the environment. The chemical properties of carbon and its compound, carbon dioxide, and the chemical and physical properties of water are unique amongst the other elements and compounds. Life as we know it on this planet could not exist were it not for the extraordinary chemical and physical attributes of a few of the commonest inorganic substances present at the surface of the earth. Henderson maintains the thesis, or paradox, that the physical world is as adapted, as unique, in these respects to the world of living things as the latter is to the physical world. In other words, the problem of adaptation is a reciprocal one. Henderson points out that if it should be found necessary to introduce an extraneous factor such as a vital force or entelechy, into the organic world to explain fitness, then by parity of reasoning an entelechy should also be postulated for the inorganic world, at the very beginning of things.

Without denying or affirming the advantage of regarding the one as being as fit as the other, it should be pointed out that the zoölogist and botanist, interested in organic evolution, and keeping within bounds, take for granted that the physical and chemical properties of the external world today have existed in essentially the same condition ever since organic evolution began its march. Evolution started with simple forms, and it has taken millions of years for the more complex forms to evolve. During the latter part of this time the external conditions seem to have been such that so far as environmental factors are concerned, the mammals, and even man, might have existed for a long time on earth before they appeared. The practical problem, then, as it presents itself to the evolutionist, is to discover how, in an environment in which water, carbon dioxide, oxygen, and a few other substances remained constant, or approximately so, the enormously varied changes in living matter came about. If the evolutionist closed his eyes to the properties of the environment, it was because he took these for granted. His unfamiliarity with the particular properties of the chemical components of the external world essential for this kind of organic evolution, may have made the biologist too optimistic and a little vague at times; but it should not be overlooked that his problem included adaptation not only to the inorganic world, but to other living things; and these other living things became as useful as water and carbon dioxide, or as dangerous as lightning. To get in touch with other animals to exploit, and to avoid being exploited is as essential for some forms of life as obtaining oxygen from the air and getting rid of carbon dioxide from the body. Let me give an example. For the aphid or plant louse a particular kind of plant at a particular time of year is essential to its life. We find that it has made the proper adjustments to suck out the juices from the leaves for food, and has adapted its mode of propagation so that it emerges from the egg at the time of year when the leaves are young and succulent. On the other hand, there is another species of insect, a small wasp, whose existence depends on finding the aphid. This wasp deposits its eggs within the body of the aphid. The larva that hatches slowly destroys the aphid, but not until the aphid has supplied the nourishment necessary for the wasp's own growth. Now, all the elaborate properties of the plant are essential to the life of the aphid, and those of the aphid to the parasitic wasp. In an outworn phraseology it might be said that one was preordained as food for the other, and the last in the chain, the parasite, might contend—if it had a mind to philosophize—that the aphid and the plant had been prepared for its advent. The fitness of the plant for the future aphid and the fitness of the aphid for the wasp is as essential, in generalization about evolution, as the fitness of the inorganic world. I venture to think that even though it greatly complicates the solution to introduce questions of this kind, it puts the emphasis where the naturalist finds it. Furthermore, introducing the theme of the destructiveness of natural processes serves as an antidote to a common implication that nature may have been "arranged" to carry out only beneficent acts. By this diversion I do not wish to minimize the interest of Henderson's speculation. The facts he elaborates are important, but they constitute only a part of the problem that the evolutionist has to solve.

There is another question running under the surface of what has just been said that I should like to mention, since it brings us back finally to the same point of view. Let us call it the lock-and-key puzzle. There is a faint suggestion of it in what Henderson says about the fitness of the environment, although he carefully refrains from saying outright that there is a sort of preordained harmony between the chemical constitution of the organism and that of the environment. It is, in fact, extremely difficult, owing to the way in which language has been formed, to avoid by implication this suggestion, however much one may wish to do so.

A recent speculation called "emergent evolution" has attracted some popular attention and is related to the present topic. There is nothing essentially new in the idea, as Wheeler has pointed out. It is frankly metaphysical, and was so considered by its earlier advocates. But it has recently been brought to the fore again by C. Lloyd Morgan in his book, *Emergent Evolution,* and given an importance which I think is not justifiable. Lloyd Morgan is aware of the metaphysical implications. The theme might well have been left to philosophers, were it not that a few biological writers have seized upon it and so interwoven it in their biological speculations that an unwary reader might suppose that emergent evolution is both a new and an important contribution to science. Lloyd Morgan says that it is the business of science and of *philosophy* to *describe* the *orderly sequence* of events in the world in which we live. "But the orderly sequence, historically viewed, appears to present from time to time something genuinely new. Under what I here call emergent evolution, stress is laid on this incoming of the new. Salient examples are afforded in the advent of life, in the advent of mind, and in the advent of reflective thought. But in the physical world emergence is no less exemplified in the advent of each new kind of atom, and of each new kind of molecule. It is beyond the wit of man to number the instances of emergence. But if nothing new emerge —if there be only regrouping of preëxisting events, *and nothing more*—then there is no emergent evolution."

Notice that Lloyd Morgan says the advent of each new kind of molecule is an emergence. This implies not only that the first time hydrogen and oxygen combined emergence took place; but that forever afterward when the process occurs to form water there is emergence. Emergent evolution is going on at such a stupendous rate around us that we are overwhelmed at the thought. But this is nothing more than a re-statement of an old commonplace of science, that water has properties that *we* might not have been able to predict from our present knowledge of hydrogen and oxygen. To assert that science will never be able to make this sort of prediction is to assume a grave responsibility, even for a philosopher. The properties of some of the missing elements in the periodic table were surprisingly well foretold many years before the discovery of the elements. Moreover, there are many organic molecules that form series of progressive complexity. In the absence of one of them (except the first), many of its properties could be approximately foretold from a knowledge of the rest. It seems to me very dubious whether anything is to be gained for science—and perhaps not even for philosophy—by resting one's faith on such dogmatic statements of the limitations of scientific accomplishment. To be fair I think I should quote a statement by Lloyd Morgan which shows where he wishes to draw the line between science and philosophy.

"The naturalistic contention is that, on the evidence, not only atoms and molecules, but organisms and minds are susceptible of treatment by scientific methods fundamentally of like kind; that all belongs to one tissue of events; and that all exemplify one foundational plan. In other words the position is that, in a philosophy based on the procedure sanctioned by progress in scientific research and thought, the advent of novelty of any kind is loyally to be accepted wherever it is found, without invoking any extra-natural Power (Force, Entelechy, Elan, or God) through the efficient Activity of which the observed facts may be explained. The question then arises whether such scientific or naturalistic interpretation suffices, or whether some further supra-naturalistic explanation is admissible at the bar of philosophy, not as superseding but as supplementing the outcome of scientific inquiry. I shall claim that it is admissible, and that there is nothing to emergent evolution, which purports to be strictly naturalistic, that precludes an acknowledgment of God. This implies (1) that a constructive philosophy is more than science, and (2) that such acknowledgment is here to be founded on philosophic considerations only."

With much in this paragraph one need not stop to quarrel—not even with the capitalization of Power, Force, Entelechy, Elan, or God; nor need we try to decide whether constructive philosophy is *more* than science, or wherein lies its more-ness. For our present purposes this escape into metaphysics or philosophy eludes us, for it is certainly *more* than the field in which biologists are engaged.

Therefore I cannot agree with Jennings' recent statement, that the acceptance of emergent evolution makes a very great difference in our attitude towards science, and biological science in particular: ". . . in the object and practice of science, in the temperament and bearing of the man of science, in the relation of science to life, and on one's general outlook on life and the universe." * I find it difficult to admit that the acceptance of this metaphysical doctrine completely transforms our whole attitude to science and life and the universe. Let me then attempt to state the reasons why we are not called upon to adopt a metaphysical philosophy over and beyond the procedure of experimental science as understood in its broadest aspects.

Biology began by describing the multitudinous forms of living things. They were classified at first according to arbitrary standards, but with the advent of the theory of evolution they were arranged according to their supposed relationships. On the theory of natural selection it was then supposed that the diversities were due to breaks in the original continuity. With the further discovery of discontinuous variation (mutation) of the primary elements (giving the basis for inherited variation) it became apparent that the earlier doctrine was erroneous and that a new conception was necessary to account for the resemblances on which classification of the material was possible. The explanation offered at the present time is that, while the emergence of new genes accounts for new variations, the effects of a new gene, changing one or many of the original characters, are superimposed upon the old background—the product of thousands of the original genes that still remain. In this way the resemblances and differences amongst living forms may be explained. These postulates do not carry the problem outside the range of observed phenomena on the biological level.

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* Hans Driesch has given a more profound philosophical analysis of emergent evolution in his address before the Sixth International Congress of Philosophy.

This stage in the development of biology involved the introduction of the experimental method. If by "experiment" we mean no more than that each individual be subjected to all possible environmental conditions and its responses recorded, we have lost sight of the essential purposes of the procedure where the intention is to discover the single components of which certain kinds of reactions are the result. Without this end in view experimentation has no more value than any other kind of simple description. While something new may be discovered by reporting everything that happens in a novel situation, and while in this haphazard way new relations may accidentally come to light, the procedure falls far short of the scientific method of experimentation by means of which complex phenomena are analyzed into simpler components. This may be carried out either on the biological level of observed or discovered relations, or by resolving the problem into physicochemical terms. Pavlov's work on conditioned reflexes is an excellent example of experimental procedure that remains strictly on the biological level. Another illustration is found in the separation of the chromosomes at the time of maturation of the germ-cells, which furnishes a simple explanation of Mendel's two laws of heredity. The observed changes that occasionally take place in the re-arrangement of the chromosomes in the germ-cells explain the alterations in the inheritance of the linkage groups of genes. Thus the laws of heredity, determined by experimental breeding, find a solution in the known rules and exceptions of chromosome behavior.

It would be more than shortsighted if biologists refused to consider the application of physical and chemical knowledge to the solution of their problems, especially wherever the biological analysis has reached a point at which chemical and physical analyses may become possible. It is unnecessary to labor the point, since a great part of our knowledge of physiology rests on information of this kind. The only dispute which might arise amongst scientists is one connected with the attempt to show that a given reaction to a physical agent—such as light, heat, gravity—approximates quantitatively to expectation based on accepted laws of physics, as in the Roscoe-Bunsen law and the rate of reaction and temperature. The story is a long one and not yet finished, but even when agreement is not as close as might be expected, the presumption remains that all the conditions under which a given reaction is occurring in living things have not been taken into full account.

Modern biology, then, rests its case on the assumption, sometimes amounting to a conviction as the result of wide experience, that the properties of living things are the outcome of their chemical and physical composition and configuration. This is not the same as saying that all the properties of living things can be explained by the known laws of chemistry and physics; for the kinds of reactions that take place in living matter are as much dependent on the kind of system involved as are reactions of non-living matter in different systems.

CHAPTER XII

MECHANISTIC AND METAPHYSICAL INTERPRETATIONS OF BIOLOGY AND OF EVOLUTION

IF the causal factors of variations that are inherited were known, it might be quite unnecessary to consider ultra-naturalistic arguments that attempt to give an "explanation" of evolution. But it cannot be said that the causal factors of such variations have been discovered. On the other hand, it cannot be claimed that the physical problem has been shown to be beyond the reach of experimental science. So long as biologists with mechanistic leanings will not admit that they have run into an impasse, philosophers will probably continue to offer a different kind of solution. In fact, it has been suggested more than once that evolution is not a problem for science at all. This assertion should at least arrest attention, for, if evolutionists are chasing a will-o'-the-wisp, the sooner we confine our attention to our legitimate field, the more conciliatory will be our attitude toward those offering other solutions.

The main question, then, is how far evolution can be studied successfully by our present experimental methods. Does the use of such methods demand the assumption of causal agents in evolution as the term is understood by physicists and chemists? For example: if the origin of heritable variations transcending the original range of variation is the central problem of evolution, have we found the causal origin of such variations to be within the reach of investigation based on mechanistic principles?

It is true that, even without this information, the theory of evolution could be accepted, because it is consistent with a large body of factual evidence, and because it has been shown that heritable variations, transcending the original boundaries, do arise at times, although at present an explanation of the causal origin of these mutations is not known. But the history of the theory of evolution has shown that biologists have never been content to stop their inquiries at this point. The search for the causal factors has never been entirely forgotten. In fact, it is exactly those theories that *seem* to offer any kind of explanation, even ultra-physical ones, of the changes that bring about evolution that have attracted most attention. The mutationists have been, on the whole, either non-committal or frankly speculative on this point. Nevertheless, the implication is not far off that new mutations are due to natural processes.

A critical examination of the different attempts to discover these causal factors shows, as I have said, that they have not been found. But with every advance in our knowledge of the chemistry and physics of living material, the possibility of finding a naturalistic explanation seems improved. By patience and industry and intelligence, biologists hope to advance their work. But so long as they have not found convincing evidence, it is an "open season" for philosophers, who are too impatient to wait, but must add the biological field to their speculations.

Fundamentally the whole question of the limitations of science is involved. Aware of the enormous labor and thought that has gone into each advance science has made, the biologist is more than skeptical when philosophers explain away by fiat his difficulties, and he is not unaware that step by step the progress of science has forced magic and metaphysical speculations farther and farther out of his field.

It is true that the facile solutions that philosophers offer make a wide appeal to the public, while the partial and incomplete answers of science make no such appeal. But, persuaded that scientific procedure is the safest one to follow in an understanding of the world which reaches us through our perceptions, and is the most useful procedure which man has found for controlling his environment and directing his welfare, the scientist often turns a deaf ear to the fine-spun arguments of the metaphysician and looks upon them as a real danger threatening the progress of science.

Metaphysicians, dissatisfied with the limitations that science would place on human speculation, appeal to the human mind as a tool capable of contributing more than the scientific method can offer. Hence we meet not infrequently with the assertion that science has its own field in which it may be expected to continue to labor without appealing to metaphysics, while metaphysics has also its field, wide enough to incorporate all that science may offer, but taking up the problems where science stops.

This convenient classification of the field of human thought and activities seems to me only a clever makeshift—an attempt on the part of metaphysicians to appear broadminded and liberal and even generous. What I find difficult to accept is, first, the limitations placed on exploration by scientific methods, and second, the assumption that the methods of science can have no bearing on the topics reserved by metaphysicians.

Such an arbitrary separation of human activities introduces an attitude that most scientists will not easily brook. It implies that the scientific method is too limited to take cognizance of certain aspects of knowledge. Of course, as long as philosophers keep their discussions just beyond the fields in which science has been successful, or has brought nature under control, just so long will unverifiable speculation be "beyond" science. But even in the fields of human conduct, science will not recognize the "right" to refer all such questions to ultra-naturalistic agencies. While it is true that most of our conduct follows the rules and conventions of the societies in which we have been brought up, many scientists accept them either perforce, or pragmatically as opportunists, or because they recognize that many of the essentials of these doctrines rest on ethical principles that are temporarily advantageous to the well-being of human society.

Having put the case for science, perhaps too aggressively, let me attempt to undo the dogmatic impression my statements may have given. So long as physiologists cannot bring within their scope all the manifold activities of the human mind, it would be most unwise to disdain to recognize its functioning in philosophy; for to the biologist the human mind must appear as the most stupendous accomplishment of the process of evolution. Moreover, he must recognize that his own success in science has been mainly through a certain *controlled* use of this instrument. He may not trust altogether its validity, and may remain very skeptical about its actions at times, so far as they depend on introspection; nevertheless he uses it for his own purposes, and in doing so frequently follows essentially the same processes of logic, and even it may be at times the quasi-metaphysical procedure, that he distrusts when it is elaborated into finalistic conceptions of the cosmos in the hands of philosophers.

It seems, therefore, that the scientist cannot afford to be entirely contemptuous of the history of philosophic and metaphysical thought, or to assume an arrogant disregard for it, even though he will not accept fictitious solutions as a substitute for the verifiable evidence that the scientific method demands.

After this excursion, a few of the more recent philosophical speculations concerning the interpretation of living things, especially those that relate to causal agents of evolution, may serve to give point to these generalities.

The difference between the kind of evolution due to the degradation of energy shown by inorganic systems on the earth's surface, and the constructive evolution shown by living things, has been made the basis of arguments purporting to show that the two kinds of changes differ fundamentally from each other. It is said, for example, that the degradation of energy is as characteristic of inorganic changes as the upbuilding of organic systems is characteristic of living things. In so far as these are antagonistic phenomena, the emphasis laid on this contrast is important, but that they are irreconcilable is by no means established. Let me illustrate by a few examples.

The evolution of the green plants was possible through the utilization of the energy of the sun to build up more complex molecules. In a rough way we say that carbon dioxide and water are combined to form starch in the presence of chlorophyll. In consequence the green plant is able to store up a supply of energy; yet when the entire system is considered, i.e., sun plus plant, the total utilizable energy may have decreased. In order to contrast living and inorganic systems it would be necessary to obtain information on isolated systems including living things, such as has been obtained on isolated inorganic systems. The evidence in hand suffices to show at least that the burden of proof is with those who deny that organic systems belong in the same category as inorganic systems. Simply to deny that they are on the same footing, as Smuts, for instance, has done, will not suffice to settle the question.

On examination, then, this contrast does not in itself appear to carry great weight. The constructive processes of living things, their upbuilding, have not been shown to call for principles that transcend physical and chemical laws. To this extent, at least, the contrast of the inorganic and organic world may not seem to carry us beyond the possibilities of mechanistic interpretations. Let us turn, then, to more scholastic distinctions.

The physiologist, J. S. Haldane, has insisted not only that the mechanistic interpretation of living things is insufficient—although justifiable within its sphere—but that it fails to take account of the most essential and characteristic feature of living things. He insists that the chief feature of animals and plants is the internal equilibrium they maintain in an ever-changing world around them; it is their self-regulating or self-adjusting power that sharply marks them off from inorganic systems. Haldane makes no claim for this as a new doctrine, but only that in the age when mechanism has had so many triumphs, the essential phenomena of life have been forgotten or brushed aside. Coming from a physiologist who has himself made important contributions to science by the application of physics and chemistry to the composition of the blood and to respiratory adjustments of animals, as well as in other fields of physiology, this pronouncement calls for consideration. It is useless to attack the argument on the grounds that it offers not a single suggestion as to how such a phenomenon as self-regulation can be approached in any other way than that in which he himself has studied it. But when Haldane places an important biological phenomenon—the self-regulatory processes—beyond the ultimate reach of science, a serious issue is enjoined.

Not only does Haldane reject mechanism as a sufficient method for the study of life, but he rejects the doctrine of vitalism as well. The time has come, he says, for giving decent burial to the mechanistic theory of life in the same grave with the vitalistic theory. But when we inquire further into Haldane's reasons for rejecting vitalism, his arguments are not so clear. He admits that "vitalism has rightly taught us that we cannot neglect the essential element of holism or coördination in life." He speaks of the orthodox vitalism of the last century, that assumed the bodies of living organisms to be the seats of activity of a special influence, the vital principle, and affirmed that to this influence, acting on lifeless matter, the coördination in structure and behavior is due. But he adds that this assumption is to be rejected for a very good reason, namely, that any physiological activity is dependent also on conditions in the environment, and is therefore partly under external influences. Hence an internal, vitalistic agent cannot account for the facts. The environment is also a part of the coördination. A clever vitalist should, I think, have little trouble in upsetting this questionable argument.

The biochemist, Henderson, who has a broad interest both in physiology and in philosophy, discussed in his book on *The Order of Nature* the self-regulatory properties of organisms. His analysis is an outstanding contribution to the subject. Henderson points out that physiologists in their analytical researches have dealt exclusively with physical and chemical phenomena of organisms as they find them, rather than with organization itself. Their method of research into the factors of organization has obscured the larger biological problem. He points out, nevertheless, that contributions from several sources have been made which involve the idea of a self-regulating organization. He recalls in this connection the work on respiration, the processes of digestion, the action of hormones and the function of the glands of internal secretion. To these is to be added the integrative action of the nervous system and the equilibrium in the blood. Most of these researches, purely physico-chemical in their intention and procedure, make it clear that "within certain limits the existence of these equilibria is essential to the preservation of life itself. . . . In other words, the task of the investigator has been to make known the facts concerning the regulation of the ultimate physical and chemical constitution of the organism." As a reservation Henderson adds: "I should be sorry to produce the impression that this idea of regulation is well defined in general physiology. The fact is that current views upon the subject are very generally loose and perhaps in part contradictory. But it is certainly rigorously defined in some departments of science. And it is unquestionably everywhere in use." He admits that "it may be at once conceded that nobody has ever given a mechanistic explanation of a single organic regulatory process. In spite of this, however, many simple mechanical analogues like the thermostat and the gyroscope are well known." As an explanation of the present state of the question, he considers "the regulation of the temperature of the human body. There exists an admirable description of the various methods by which the tendency to a rise or fall of temperature is counteracted. Conduction, convection, and radiation of heat and the evaporation of water are all involved.

These are varied according to the condition of the organism and its environment. The process is controlled in a most intricate manner through the operation of physiological activities such as the distribution of the blood in the different parts of the body and the intervention of the sweat glands. Beneath these conditions in turn is the regulation of the production of heat, which, at need, rises and falls so as to preserve the equilibrium. Under ordinary circumstances the oxidation of carbohydrate alone may be concerned in this fluctuation, but, if the supply of carbohydrate fails, other substances will be employed in its stead. Moreover, all of these processes are involved in and modified by other physiological activities such as the performance of mechanical work."

"Clearly," Henderson says, "the physiologist is here confronted by an incomplete, but yet partially successful mechanistic account of one element of the functional organization of the human body. But how is the process governed? By what chain of mechanical causation does a fall in the temperature cause a rise in the rate of oxidation? This question, in turn, is not altogether beyond the scope of our present physiological investigations. But sooner or later, when the problem is studied, we come upon the fact that a certain organ or group of cells accomplishes that which is requisite to the preservation of the equilibrium, varying the internal conditions according to the variation of the external conditions, in a manner which we can on no account at present explain. The same difficulty is encountered in the analysis of every other organic regulation, of whatever sort. There is no physiological phenomenon of regulation, the autonomy of which we can today understand." Thus Henderson runs down part of the ultimate self-regulating mechanism to the cells of the body itself, and he contends that no one knows, as yet, how the cell manages to bring this regulation about.

Haldane, working with systems and organs, failed to see that for want of just this knowledge his analysis came to a standstill. Curiously enough he went to the other extreme and concluded that "the organism as a whole" is responsible for self-regulation. It may, indeed, be true that the classical physiology has been "slowing down," because it dealt with large organ systems and neglected to push its investigation into the cell itself. Today a new group of investigators is growing up, who are studying just these physiological properties of cells, already with great promise of success.

In the last chapter, Lloyd Morgan's argument for emergent evolution was discussed. It may be appropriate here to refer to a similar speculation by General Smuts, which he calls Holism, or the Doctrine of Wholes. Inasmuch as Smuts, like Haldane, rejects both mechanism and vitalism, neither doctrine being sufficient to explain life, I have deferred till now a consideration of his polemic. Vitalism, he says, is still "the view mainly held by common sense, while mechanism still persists as the creed of many scientists. . . . Vitalism is nothing but an anachronism, a survival of the animism of primitive man, who believed in semi-material spirits inhabiting and animating not only animals but also trees and even inanimate objects." Vitalism, Smuts affirms, is obsolete and mechanism obsolescent. Although mechanism is obsolescent it still serves a useful purpose in the search for detailed physiological mechanisms. The mechanical model is dead as a dodo. People forget that it is a mere hypothesis: "they accepted it as a reality; they applied it even to life and mind." It "became not the symbol but the very soul of reality."

"And so we come to the concept of Holism. Holism marks an attempt to read the riddle of evolution more closely. The evolution of the material universe, and of life on this globe seems to be, in part at least, a negation of the second law of thermodynamics, the law of the dissipation of energy." Organic evolution "shows us a universe which in many respects has for thousands of millions of years, been on the upgrade," etc.

"In all this evolution we see the second law of thermodynamics upset; we see the law of the logic of science apparently violated. We see the more coming out of the less, the something out of the apparent nothing; the higher out of the lower; the complex, more valuable, out of the simpler, less valuable. . . . I suggest that we have to jettison Mechanism and its logical implications. We have to adopt the idea of the whole." Thus he eloquently throws overboard the mechanistic viewpoint. We need not follow the General in his rather naïve ideas as to the life of the cell, chromosomes, Golgi bodies and the genes: but we may well question the dictum which he lays down with so much assurance that the second law of thermodynamics is upset. It is true that the second law of thermodynamics applies with less probability the smaller the system; nevertheless it remains to be proven that in living things we are dealing with systems so small that it does not apply. Moreover, as explained above in connection with chlorophyll and photosynthesis, there is evidence to the contrary.

On the principle that it takes a metaphysician to catch a metaphysician, let me quote a real vitalist, who, proclaiming himself as such, proceeds to express with equal vigor his opinion of the views of Haldane and Smuts. I refer to H. W. Carr, who took part with the former in a recent debate on "The Nature of Life":

"Both General Smuts and Doctor Haldane are as convinced as I am of the failure of mechanism. They, however, will not accept vitalism. What, then, is their alternative? Is it not to reject, as I do, the natural precedence of matter to life, and of life to mind? General Smuts accepts these 'emergent levels' and takes them at their face value, and accounts for their mysterious emergence by postulating a principle which for some inexplicable reason is making for wholeness. The triumph of this principle is marked, he tells us, by the successive arrival of the atom, the cell, the personality. Dr. Haldane is entirely in accord with me in rejecting this emergence theory. The emergence, as he has shown in his Gifford Lectures, is not of something new, but of something present from the first. . . . My vitalism is a metaphysical theory. . . . For me its reality is activity, and activity is distinguished from mechanical movement by its individuality. Anything is what it does, and what does nothing is nothing. . . . Life and mind are, therefore, of the essence of reality. They are not late-comers; they are there from the first."

Carr calls his doctrine vitalism. He suggests that General Smuts chose the wrong word for his doctrine when the right word was staring him in the face. While this word is vitalism, it is not the vitalism of Bergson and of Driesch (which Carr calls a perversion of the original Aristotelian entelechy), but a concept which makes life and living original, which includes matter and life in the concept of life, instead of generating life out of matter, and mind out of life.

As I have said, there need be no argument with scientists so long as mystics calling themselves philosophers discuss life and evolution as metaphysical convictions. But when they go out of their way to condemn the principle of mechanism, and imply that scientists are overlooking their real problems and frittering away their time on trivial matters, it is only human, I think, if scientists try to find some justification for their procedure.

But before undertaking this defence, there is one more topic to consider that has recently troubled the calm waters of science under the name of *Organicism.* For many years a controversy has been going on between those who have studied the functions of individual organs of the body, and those who insist that the organism is a whole and must be studied as such—or, as they sometimes put it, an organism is more than the sum of its parts. Even so radical an experimentalist as Claude Bernard, who made use of strictly mechanistic procedure in his work, believed that, while the functioning of each organ depends on the general forces of nature, yet when taken in connection with others, it is directed by some invisible guide. The problem of the physiologist is with matter and not with the first causes "or the vital forces derived therefrom. . . . Determinism can never be but physico-chemical determinism. The vital force and life belong to the metaphysical world."

This idea that "the harmonious character of the whole" is something beyond the reach of scientists has repeated itself over and over again since the time of Claude Bernard (1813–78).

A philosopher and mathematician, Whitehead, has discovered that the method, familiar to biologists, of studying the organism as a whole is far superior to the method of the chemist and the physicist, who study the parts of systems and neglect the wholes. Furthermore, the interest shown in recent years in trying to reduce biological phenomena to chemistry and physics is misplaced, or second-rate, for the chemistry and physics of a molecule or an atom within an organism is something different from its behavior, or at least its "relatedness," outside this system. This means, I take it, not that the laws of chemistry and physics are abrogated, but that new laws, relatednesses, now exhibit themselves, and it is these that concern the biologist.

Whitehead says: "A thoroughgoing organic theory of nature enables us to understand the chief requisites of the doctrine of evolution. The main work, proceeding during this pause at the end of the nineteenth century, was the absorption of this doctrine as guiding the methodology of all branches of science. By a blindness which is almost judicial as being a penalty affixed by hasty, superficial thinking, many religious thinkers opposed the new doctrine; although, in truth, a thorough-going evolutionary philosophy is inconsistent with materialism. The aboriginal stuff, or material, from which a materialistic philosophy starts, is incapable of evolution. This material is in itself the ultimate substance. Evolution, on the materialistic theory, is reduced to the rôle of being another word for the description of the changes of the external relations between portions of matter. There is nothing to evolve, because one set of external relations is as good as any other set of external relations. There can merely be change, purposeless and unprogressive. But the whole point of the modern doctrine is the evolution of the complex organisms from antecedent states of less complex organisms. The doctrine thus cries aloud for a conception of organism as fundamental for nature. It also requires an underlying activity—a substantial activity—expressing itself in individual embodiments, and evolving in achievements of organism. The organism is a unit of emergent value, a real fusion of the characters of eternal objects, emerging for its own sake.

"Thus in the process of analyzing the character of nature itself, we find that the emergence of organisms depends on a selective activity which is akin to purpose. The point is that the enduring organisms are now the outcome of evolution; and that, beyond these organisms, there is nothing else that endures. On the materialistic theory, there is a material—such as matter or electricity—which endures. On the organic theory, the only endurances are structures of activity, and the structures are evolved.

"The concrete enduring entities are organisms, so that the plan of the *whole* influences the very characters of the various subordinate organisms which enter into it. In the case of an animal, the mental states enter into the plan of the total organism and thus modify the plans of the successive subordinate organisms until the ultimate smallest organisms, such as electrons, are reached. Thus an electron within a living body is different from an electron outside of it, by reason of the plan of the body. The electron blindly runs either within or without the body; but it runs within the body in accordance with its character within the body; that is to say, in accordance with the general plan of the body, and this plan includes the mental state. But this principle of modification is perfectly general throughout nature, and represents no property peculiar to living bodies."

If the biologist finds it difficult to grasp this philosophical magnificence, and turns to the astrophysicist Eddington, he may be further confused. Eddington says "I regard a mechanistic theory of mind and consciousness as entirely nonsensical; consciousness is utterly incommensurable with anything which the physicist is looking for in the world by his method of exploration." He continues: "But I have not the same fundamental objection to a mechanistic theory of life.

. . . I am content to leave it an open question to be decided ultimately by biological evidence."

In a third statement of Eddington's I think there will be less ground for distrust, namely, that the word mechanistic is to be understood in a very modernistic sense. "In an older and stricter sense we can no longer admit a mechanistic theory of the atom, much less a mechanistic theory of life. I take 'mechanistic theory' now to mean that the phenomena of life admit of the same kind of treatment and analysis as is applied by physicists to the phenomena of the inorganic world, so that they do not require any more transcendental agencies or conceptions."

I need not repeat that the biologist arises from reading of this literature in a puzzled frame of mind. He is told that the biological conception of the organization is the correct one; that instead of biology being reduced to the atomistic view of the chemist and physicist the reverse is true, that physics has adopted the biological view. It is reassuring, perhaps, to be told by Eddington that "holism is not inconsistent with mechanistic theory," and "that to say, 'the whole comprises something more than the sum of its parts' is logically nonsensical; but we may agree that, if we divide an object spatially (as we ordinarily do) the spatial parts do not necessarily constitute the whole."

There have been in the past two doctrines of evolution that have run independent courses: one was concerned with the evolution of the stellar universe, the other with the evolution of living things. To these two there has been added in recent years, the evolution of the materials themselves of the universe of atoms out of electrons and protons. New mathematical principles have been proposed, some of which are strangely different from the older mechanistic systems. It may seem dogmatic, therefore, to urge that, even on the mechanistic level, there remains still a great field of work open to biology. When the physicists have come to some common agreement, and are prepared to offer some workable theory concerning the properties of the kind of matter in the systems with which biologists have to do, biologists will no doubt willingly take over the new physics and apply it to their own field, whether it is called mechanistic, or by some other name.

In conclusion I should like to enter a mild protest against a common indictment of biology which introspective philosophy not infrequently employs. Assuming that the mechanist is searching for a finalistic solution of the cosmos, philosophy condescendingly points out that the mechanistic procedure is inadequate to give this solution. Having routed the supposed pretensions of the mechanist, or, at most, allowed him a limited field for his endeavors, the grander theories are then proposed. Now it is unfair to put this burden on the poor mechanist. He is not pretending to explain the universe. Mechanists make no such claims. They do claim, however, that science has greatly profited by the use of the mechanistic approach in the widest sense, and they resent the boundaries set to their progress by metaphysicians. They even question the finality of the decisions of the metaphysicians. The boldest spirits amongst the mechanists go further and claim that in time they hope to bring within reach of their methods a study of the lucubrations, hallucinations, and obsessions of the human mind which, masquerading under the illumination of introspective metaphysics and transcendental philosophy, pretends to solve all the riddles of the universe.

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INDEX

Acquired characters, 187, 202.
Adaptation, 111–131.
Agar, 23.
Agassiz, Louis, 173.
Albinism, 204.
Andalusian fowl, 187, 188.
Antibodies, 194.
Antirrhinum, 37.
Ascaris, 24, 25.
Attached-X, 82.
Axolotl, 177.

Von Baer, 172, 173.
Bateson, 18, 56, 183.
Batracoceps, 49.
Belling, 89.
Benoit, 160.
Bergson, 226, 249.
Bernard, Claude, 250.
Bernstein, 147, 148.
Bidder's organ, 161.
Blakeslee, 27, 28, 90.
Blood groups, 147.
Bolk, 177, 178.
Bonellia, 161.
Boycott, 46.
Brachydactyly, 205.
Brassica, 30.
Bridges, 76, 79, 81, 189.
Bridges and Morgan, 79.
Buffon, 220.

Capon, 157.
Capsella, 136.
Carl-Saunders, 194.
Castle, 97–100.
Castration, 157.
Caterpillar, 164.
Cell division, 23, 24.
Cell-plasm, 45, 46.
Chlorophyll, 48.
Chromosome map, 76.
Chromosome rings, 87, 88.
Chromosomes, 22–28, 44, 45.
Cleland, 88–90.
Color-blindness, 206.
Conditioned reflex, 223.
Conjugation of chromosomes, 49.
Crepis, 24, 25.
Cross-fertilization, 94.
Crossing-over, 50, 70–78.
Cross-over suppressor, 82.
Cuvier, 220.
Cytoplasm, 47.

Darwin, 61, 91, 95, 109, 111, 120, 152–156, 173, 197, 216, 217, 227.
Datura, 24, 25, 27, 28.
Delphinium, 136.
Demerec, 135, 136.
Descent of Man, 153.
Diver, 46.
Dobzhansky, 80–86.
Dominant character, 39, 40, 63.
Domm, 160.
Driesch, 183, 234, 249.
Drosophila, melanogaster, 24, 25, 33–37, 50, 57, 58, 71, 72, 77, 80, 82, 100, 134, 135, 141, 165, 187–189, 196.
Drosophila virilis, 135, 136.
Dubinin, 138, 139.

East, 100.
Eddington, 114, 252, 253.
Eggs, number of, 121–123.

Emergent evolution, 231, 232.
Emerson, R. A., 134, 135.
Emerson, S., 190.

Fertilization, 55, 56.
Findlay, 190.
Fisher, 141, 142.
Four o'clock, 65, 66.

Gaertner, 61.
Galton, 18, 143, 145.
Galton's law of ancesteral inheritance, 144–146.
Gene, 44, 59, 137–139.
Gene mutations, 32.
Genetic and physical maps, 86.
Gill-slits, 174, 175.
Goldschmidt, 166, 167.
Goodale, 159.
Griffith, 194, 195.
Guinea-pigs, 100, 200.
Guyer, 193, 194.
Gynandromorphs, 168.
Gypsy moths, 166, 167.

Haeckel, 173.
Haldane, J. B. S., 142.
Haldane, J. S., 243, 244, 247, 249.
Henderson, 229, 231, 244, 246.
Heteroploid, 27.
Hexaploid, 29.
Holism, 247, 248.
Hormones, 152, 157, 161, 169.
Horns, 163.
Horse, evolution of, 112.
Huntington's chorea, 210.
Huxley, 194.
Hybrid vigor, 104.
Hydatina, 121.

Identical twins, 207.
Ikeno, 135.

Imai, 135.
Inbreeding, 99.
Indian corn, 101, 103.
Infertility, 105, 106.
Intelligence, 208, 209.
Intracellular pangenesis, 18, 45.

Jansky, 148.
Janssen, 49, 94–97, 99.
Jeans, 14.
Jennings, 234.
Johannsen, 13.
Jones, 101, 102.
Jordanons, 21.

Kammerer, 193.
Karpechenko, 30, 31.
Karr, 248, 249.
Kielmeyer, 172.
King, 100.
Knight, 61.
Köllreuter, 61, 104.
Kopec, 164.
Korschinsky, 18.
Kropotkin, 119.

Lamarck, 188, 189, 220, 221.
Lamarck's evening primrose, 21.
Landsteiner, 148.
Lebistes, 37.
Lewis, 225.
Linkage, 70, 71, 90.
Linnaeus, 21.
Linnean species, 21.
Ljungdahl, 30, 31.

McClintock, 50.
McDougall, 199, 200.
Maize, 33, 135, 141.
Malpighian tubules, 196.
Man, 25, 203.
Map-distance, 78.

Map of chromosomes, 76.
Maturation of egg, 54.
Maturation of germ-cells, 48–53.
Maturation of sperm-cells, 53.
Maupas, 125, 126.
May, 135.
Meckel, 172.
Mecostethus, 24, 25.
Meiosis, 49–54.
Mendel, 13, 61, 64.
Mendel's first law, 64.
Mendel's second law, 66, 69, 70, 89.
Mendel's theory, 43.
Mimicry, 115.
Mirabilis, 65, 66, 136.
Mohr, 81.
Morgan, C. Lloyd, 232, 233, 247.
Morgan, L. V., 81.
Mott-Smith, 81.
Muller, 55, 57, 58, 78, 81–83, 207.
Multiple allelomorphs, 34, 138.
Mutant types, 40.
Mutation, 132–151.

Nabours, 37.
Natural selection, 109, 131, 148–150, 153, 220, 227.
Naudin, 61.
Newman, 207.
Notch–8 deficiency, 81.

Octoploid, 29.
Oehlkers, 88.
Oenothera Lamarckiana, 19–21, 25, 26, 88–90.
Oken, 172.
Organicism, 250.
Origin of Species, 19, 153.
Ottenberg, 148.
Oyster, 121.

Painter, 82, 83.
Paleontology, 185.

Pangenesis, 197.
Paratettix, 37.
Patterson, 57.
Pavlov, 223, 235.
Pea, 25, 63, 64, 67, 68.
Pentaploid, 29.
Pézard, 160.
Phytodecta, 37.
Plantago, 135.
Plastids, 48.
Plunkett, 82.
Point mutation, 39, 55.
Polar bodies, 54, 55.
Polyploid, 29, 30.
Poppy, 30, 31.
Propagation, 120.
Protective coloration, 115.
Punnett, 56, 121.
Pure lines, 95.

Rabbit, 193.
Radium, 79, 81.
Raphanus, 30, 31.
Rats, 97, 98, 100, 195, 199.
Recapitulation theory, 172.
Recessive characters, 39, 40, 63.
Reciprocal hybrids, 47.
Reduction, 51.
Rejuvenation, 125.
Reversal of sex, 160.
Rotifer, 177.
Roux, 179.

Salmon, 121.
Scute, 138.
Secondary sexual characters, 152, 156, 162.
Selection theory, 95, 97, 98.
Self-fertilization, 102, 103.
Serebrovsky, 138, 139.
Sexual reproduction, 125.

Sexual selection, 152–155, 165, 169.
Shull, 100.
Smuts, 243, 247–249.
Snails, 46.
Social evolution, 203.
Spermatogenesis, 52.
St. Hilaire, 220, 221.
Stag, 163.
Sterility, 106–108.
Stern, 50, 81.
Stockard, 200.
Sturtevant, 46, 78, 81, 82, 90.
Sumner, 195.
Survival of the fittest, 110, 120–124.
Sutton, 13, 69.
Sweet pea, 141.

Täckholm, 29.
Tetraploid, 27–29.
Timofeëff–Ressovsky, 57.
Translocation, 82–87.
Trifolium, 30.
Triploid, 27–29.

Variability, 92.
Vicari, 99.
Vitalism, 247, 249.
De Vries, 13, 18–22, 27, 45, 109, 183.

Wallace, 153.
Walther, 172.
Weinstein, 81.
Weismann, 69, 178–180, 192.
Wheeler, 231.
Whitehead, 250–252.
Woodruff, 126.
Wright, 100, 141, 142.

X-chromosome, 73, 81–83.
X-rays, 55–58, 79, 81, 136, 201, 202.

Y-chromosome, 73, 80, 81, 85.

Zawadowsky, 160.
Zea mays, 26, 136.
Zulueta, 37, 38.

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